

INTERACTIONS OF FIRE ANTS AND XYLOPHILOUS HYMENOPTERA

by

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(Under the Direction of Robert W. Matthews)

ABSTRACT

A review of the evolutionary significance of ants to nesting behaviors expressed in social and solitary wasps and bees is presented. In response to ant predation many Hymenoptera have adopted a variety of nesting behaviors thought to reduce such predation. These include architectural defenses (e.g., pedicels or other structures that restrict access to the nest), glandular defenses, wherein a glandular product of the wasp or bee is used to repel or thwart ants, and active defenses (e.g., method of colony formation in social vespids and prey-carriage mechanisms in sphecids).

Trap-nests were used to survey the abundance, seasonal occurrence, and nest architecture of xylophilous Hymenoptera in early successional old field habitats of Georgia and South Carolina from March to September of 2001. Occupants of trap-nests included three Vespidae (*Euodynerus megaera* (Lepeletier), *Ancistrocerus campestris* (Saussure), and *Monobia quadridens* (L.)), four Sphecidae (*Isodontia mexicana* (Saussure), *Solierella plenoculoides* (Fox), *Trypoxylon collinum* (Smith), *T. clavatum* (Say), and *T. striatum* Provancher), two Megachilidae (*Megachile frigida* Smith and *Osmia albiventris* Cresson), and one Anthophoridae (*Xylocopa virginica* (L.)). This study records the first biological data for *S. plenoculoides* and *M. frigida*. The bees (*O. albiventris* and *M. frigida*) nested early in the season (April-May), whereas the vespid and sphecid wasps nested predominantly in the summer (May-August). No correlation was found for either the number of species nesting per site or the number of nests per site and abundance of red imported fire ants, *Solenopsis invicta* Buren (RIFA), or plant diversity. However, the four sites in Georgia were more floristically diverse than the four sites in South Carolina and had significantly higher numbers of occupied nests. Only *E. megaera* nested at all sites and it accounted for 35% of all completed nests. Comparisons made with trap-nest data collected 40 years earlier by Krombein (1967) in various southeastern U.S. localities revealed nest architecture and species differences that are interpreted in light of nest placement and the arrival of the RIFA. Comparing these data with similar data from trap-nesting studies in Europe suggest that placing more stations with fewer trap-nests per station increases nesting rate (i.e., placing 100 trap-nests at 50 locations will trap more Hymenoptera than placing 100 trap-nests at two locations). These data form a baseline for cavity-nesting Hymenoptera diversity of the early successional stages of an old field habitat that may prove important as habitat use changes and as non-native species, such as RIFA, become intergrated and more abundant in the region.

In another study, two groups of alfalfa leaf-cutting bees, *Megachile rotundata* Fabricius, were manipulated to nest in trap-nests at a site in Oconee Co., Georgia which was also monitored for RIFA density. When RIFA were present at lower densities there were no significant differences in nest architecture (closure plug thickness and number of cells) between nests that were close to the ground (<30 cm) and nests that were 150 cm above the ground. Nor were there significant differences in nest architecture between nests in locations where ants were excluded and nests in locations that were accessible to ants. However, when RIFA foragers were more abundant closure plugs were significantly thinner and there were significantly fewer cells in ant-excluded nests than in ant-accessible nests. Also, closure plugs were significantly thicker in nests that were close to the ground than in nests that were further from the ground. These findings suggest that these cavity-nesting bees adapt their nesting behavior in response to exposure to a novel Formicidae species.

INDEX WORDS: Cavity-nesting Hymenoptera, Trap-nesting, *Solenopsis invicta*, *Megachile rotundata*, Native Fauna, Nest architecture, Old field habitats

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DEDICATION

I would like to dedicate this dissertation to my wife, Laura Jenkins, and my brother, Daniel Jenkins. They encouraged me throughout this process and made graduate life much more bearable for me.

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CHAPTER 1

ANTS AS A SELECTIVE FORCE ON ACULEATE HYMENOPTERA: A REVIEW¹

Introduction

For the approximately 100 million years that ants have been on earth their ubiquity and sociality have made them one of the premier predators facing other arthropods, including aculeate Hymenoptera. This literature review explores the extent to which ants pose a threat to other Hymenoptera, how Hymenoptera may have evolved in response to this selective pressure, and how Hymenoptera might respond to pressure from novel Formicidae (e.g. *Solenopsis invicta* Buren, the red imported fire ant, in the southeastern United States).

Ants as Predators on Hymenoptera

The Formicidae are a successful and ubiquitous group. Out of the approximately 750,000 species of insects that have been described about 9500 are ants (Arnett 1985). Approximately 5300 individual ants were found in a single m² of soil near Manaus, Brazil (Adis et al. 1987), and 69% of the insects collected from arboreal habitats in Peru were ants (Erwin 1989). The sheer biomass of ants on this earth suggests that they are very likely to come in contact with other aculeate Hymenoptera and either consume them or compete with them for important resources.

In Costa Rica, army ants (*Eciton burchelli*) were found to have a significant impact on colonies of *Polistes erythrocephalus* (Young 1979). Persistent predation by the

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ants caused many wasp colonies to relocate (Young 1979). Once ants began plundering a nest the wasps swarmed to a different site to begin a new nest (Young 1979), suggesting that swarming behavior may be correlated to increased ant predation (Jeanne 1979; Kojima 1993).

Australian *Exoneura* bees are under constant pressure from ants (Cane and Michener 1983; Matthews, pers. comm.) and Schultz (1977) demonstrated that several species of ants are important predators of the alkali bee, *Nomia melanderi*. *Solenopsis* ants were the dominant source of larval mortality in *Bembix multipicta* (Cane and Miyamoto 1979). *Solenopsis molesta* (Say) destroyed 23% of 361 *Oxybelus subulatus* (Robertson) cells in another study (Peckham 1977) and at one site in Georgia *Solenopsis pergandi* Forel caused 13.5% of all mortality in cells of *O. sericeus* Robertson (Hook and Matthews 1980).

Ants often invade nests that are inadequately sealed (Knisley et al. 1989). *Xylocopa* and various allodapine bees (except *Allodape*) block their single nest entrance with the dorsum of their abdomen (Iwata 1976; Roubik 1989). Iwata (1976) has noted that removal of occupant bees usually results in successful ant raids within a day. Wasps in areas with dense populations of ant foragers have been found to occupy protected nests more often than they occupy nests that are accessible to foraging ants (Miyano and Yamaguchi 2001).

Impact of Ants on the Evolution of Aculeate Hymenoptera Behavior

Most researchers agree that ants have played an enormous role in the evolution of wasps and bees (Vecht 1967; Michener 1974; Jeanne 1975; Evans 1977; Hansell 1987;

Williams et al. 1986; Young 1979). However, it is difficult to experimentally test such a hypothesis, and current interactions between ants and solitary Hymenoptera may not accurately reflect the importance of ants as predators in the past (Gadagkar 1991).

The nests of Hymenoptera are veritable treasure troves to foraging ants; cells stocked with juicy grubs or sweet honey make great ant-booty. Furthermore, many Hymenoptera constantly fly into and out of their nests, requiring that the nest have at least one opening by which foraging ants may gain access. Although many researchers agree that the concentration of resources (i.e. larvae and stored food are found in larger quantities) in the nests of eusocial Hymenoptera is an important factor in the development of defenses in eusocial Hymenoptera, this is probably more important in terms of larger, vertebrate predators, such as skunks, bears, monkeys, and humans (Kukuk et al. 1989). Anti-ant defenses include nest architectural features that limit access to an easily defensible area, applications of ant-repellent chemicals to the nest (either glandular or of botanical origin), and behavioral responses to ants.

Architectural Defenses

Many wasps and bees construct nests in such a manner as to limit access to invertebrate predators. Social Hymenoptera that found nests in swarms typically enclose their nests in carton with one or a few entrances that are actively guarded (Wenzel 1991). Many wasps that found colonies independently connect their nest to the substrate with a single narrow pedicel (Spradbery 1973; Wenzel 1991). By placing baits on nests with and without pedicels and measuring the number of ants at each nest Grajales and Wcislo (1998) demonstrated that the pedicels on the nests of *Microstigmus thripoctenus* reduce

access to foraging ants. *Passaloecus cuspidatus* Smith collects beads of pine resin and smears them around the entrance to her nest before constructing it, possibly as a defense against foraging ants (Krombein 1967; Fricke 1995). The nests of some eusocial Hymenoptera are constructed of hard carton material or resins that are virtually impregnable (Skutch 1971; Chadab 1979; Roubik 1989). Stingless bees in the tropics often construct turrets or narrow entrance tubes that are easily defended (Michener 1974; Roubik 1989). *Bembix multipicta* constructs three types of outer enclosures, which vary in thickness (Cane and Miyamoto 1979). The temporary closure is thinnest and is used only when the females are out foraging (Cane and Miyamoto 1979). Of the three types of closure, the temporary closure is susceptible to raiding ants, whereas the closures made in the evening and the closures made when the nest is completed are thicker and successfully keep ants out of the nests (Cane and Miyamoto 1979). Matthews (1991) has speculated that the elaborate mound-leveling behaviors of *Bembix* and other wasps (Evans 1966a, b; Evans and Matthews 1973; Matthews et al. 1981) have evolved to disrupt chemical trails of foraging ants or to conceal the nest location.

The placement of nests can also play an important part in avoiding predation by ants (Evans and Eberhard 1970; Jeanne 1978). The vespid species *Epipona tatusa* and *Chartergus chartergoides* nest high in the forest canopy where raiding *Eciton* ants do not usually forage (Jeanne 1991). Many eusocial wasps in the neotropics nest on plants inhabited by ants in the genera *Allomerus* and *Pheidole*, presumably for the protection these ants afford against army ants (Herre et al. 1986; Richards and Richards 1951). Nests of *Parachartergus apicalis* and *Polybia rejecta* are commonly found on *Acacia* trees occupied by *Pseudomyrmex* spp. and dolichoderine ants (Dejean et al. 2001). In the

Guianese rainforest significantly more wasps (social and solitary) nest on *Astrocaryum sciophilum*, a palm with long, thin spines that act as ready-made pedicels to reduce access to ants (Dejean et al. 1998).

Glandular Defenses

Eusocial Hymenoptera in which a single female founds the new colony (e.g. some *Polistes* spp., *Vespa* spp., *Vespula* spp., and *Dolichovespula* spp.) are not able to depend on active defenses against ants early in colony development since the foundress is required to leave the nest unattended while she forages for nest materials and prey for her brood. Applications of chemical ant repellents are a common solution for these wasps (Jeanne 1970; Wenzel 1991; Keeping 1990). The independent-founding Polistinae apply an “ant repellent” from their van der Vecht’s gland to the pedicel of their nest (Dani et al. 1996; Espelie and Hermann 1990; Evans and Eberhard 1970; Hermann and Dirks 1974; Jeanne et al. 1983; Jeanne 1970) and rubbing activity appears to become more common when ants are present (Post and Jeanne 1981; Keeping 1990). However, Kudo and Yamane (1996) found that pedicel rubbing behavior occurs in *Polistes* wasps even when ants are not present and it occurs at rates similar to those occurring in wild specimens from the same latitude where the lab wasps were obtained, suggesting that there is an inherited latitudinal effect on this behavior. *Parapolybia indica* foundresses rub the pedicel in close temporal association with departure from the nest and this association is more frequent prior to emergence of workers than after workers have emerged and are able to defend the nest while foragers were off of the nest (Kojima 1992). Bees in the genus *Exoneura* rely on mandibular gland secretions to repel ants from their nests (Cane

and Michener 1983). The small neotropical wasp *Nectarinella championi* places stalks tipped with a sticky substance around their nests (Skutch 1971; Schremmer 1977). Robert Jeanne (1991) believes that the small size of this wasp precludes active defense against ants, making the repellent stalks necessary. Females of the wasp genus *Leipomeles* apply a sticky substance to the stems of leaves on which their nests are built (Evans and Eberhard 1970). This sticky substance presumably acts as an ant-guard (Evans and Eberhard 1970). Many Stenogastrinae (e.g. *Parischnogaster*) often produce abdominal secretions thought to function as ant guards (Turillazzi and Pardi 1981). The nest entrances of Meliponine bees are usually avoided by raiding columns of army ants (*Eciton* spp.) (Khoo and Yong 1987). These nest entrances are composed of botanical resins that may have ant-repellent properties, as well as antifungal properties (Michener 1974; Wille and Michener 1973; Messer 1984; Roubik 1989).

Active Defenses

Several researchers have observed the active responses of eusocial Hymenoptera to ant invasions. Honeybees exhibit an effective defensive behavior when confronted with various ant species or the chemical odors associated with these ants (Spangler and Taber 1970). The behavior entails kicking the ants, presumably to loosen their “grip,” followed by vigorous fanning with their wings (Spangler and Taber 1970). The behavior described by Spangler and Taber is remarkably similar to the behavior exhibited by *Protopolybia exigua* when confronted with ants (*Eciton* and *Camponotus* spp.) or with olfactory stimuli, such as formic acid (Chadab 1979; see also Jeanne 1991). Chadab interpreted the fanning behavior as an alarm communication, but Jeanne interprets the

fanning behavior exhibited by *Polybia occidentalis* as a physical defense; the wasps actually “blow” the ants persistently until the ants give up and leave the nest (Jeanne 1991).

When the nests of some stingless bees are harassed by ants the bees place resin from the nest around the entrance, building a protective ring against the ants (Roubik 1989). This behavior is similar to one exhibited by several species of *Bombus*, wherein the bees “daub” intruders with honey until the intruders are incapacitated (Fuller and Plowright 1986); however, this behavior has only been observed in response to other species of *Bombus* (Fuller and Plowright 1986).

Many ground nesting Hymenoptera aggressively pursue and bite foraging ants that venture too close to nests they are constructing or provisioning (Rosenheim 1988). Female *Stictia maculata* will pick up foraging ants that have entered their nest and bodily remove them (Matthews et al. 1981). This behavior is also exhibited by males of *Xylocopa* spp. (Iwata 1976; Roubik 1989), and by females of *Bembix multipicta* in Costa Rica (Cane and Miyamoto 1979). However, in *B. multipicta*, which also removed tiger beetles foraging too close to their nests, this defense was rarely successful and females often had to give up and start a new nest somewhere else once ants had discovered their nests.

Swarming may be a behavior that has evolved in response to ant predation (Matsuura and Yamane 1990). It has long been noted that in temperate areas the independent founding *Vespula* and *Dolichovespula* are the dominant social wasps but in the tropics the swarm-founding Polistinae are the dominant social wasps (Jeanne 1991 and 1979; Ihering 1896; Wenzel 1991; Wilson 1971; Kojima 1992; Matsuura and

Yamane 1983). The vast majority of social Apidae in temperate climates are members of the genus *Bombus*, in which a single reproductive female founds her nest in spring (Roubik 1989). However, the primary explanation Roubik gives for this behavior is seasonality (i.e. the winter season is better survived by single foundresses). Ants may be the driving force behind this dichotomy of colony-forming strategies between temperate and tropical regions. Kojima (1993) demonstrated that Japanese paper wasps apply more ant-repellent in tropical areas and he argues that ant predation becomes a more serious problem in decreasing latitudes, a trend also supported by other studies (Kudo and Yamane 1996). Comparisons of bait discovery rates between pasture sites in central Florida and northern Georgia suggest that ants pose a significant threat in decreasing latitudes (DAJ unpublished). Not only are baits discovered and monopolized more quickly in central Florida pastures than in north Georgia pastures, but more species of predatory ants are present (Ward 2000) and pose a greater threat at any given time of day. If ants do pose a more substantial threat in the tropics than in temperate zones this may have resulted in the two dominant ant-defense strategies exhibited by social Hymenoptera (glandular in the temperate zones versus active nest defense in the tropics). Glandular defenses may be physiologically expensive or not as effective in situations where ants are abundant and persistent. It has been hypothesized that the paucity of carrion consuming beetles, such as silphids and staphylinids, in many tropical areas may be due to the large populations of ants in these areas (Janzen 1983; Hesse 1937). Furthermore, Hesse points out that there are several vertebrates that are specialized ant predators in the tropics (armadillos, aardvarks, pangolins, the earth wolf, and echidnas) whereas this role is filled only by woodpeckers and armadillos in the temperate zones (Hesse 1937). If ants are

indeed more prevalent in the tropics, they may pose a threat to single foundress colonies of social wasps when these colonies are young, whereas swarming colonies would always have individuals present to guard the nest against marauding ants.

Polybia sericea is a swarm-founding wasp for which there is no evidence that an ant repellent is applied to the nest, suggesting that ant predation does play an important role in the mode of nest founding (London and Jeanne 2000). London and Jeanne (2000) point out that swarm-founding wasps may depend more on active defenses whereas independent-founding wasps depend more on glandular secretions to protect their nests from ants.

Evans (1963) and Evans and Eberhard (1970) argue that ants, as well as other parasites and predators, have been an important selective force influencing prey carriage in the Sphecidae and other wasps. Pompilid and Ampulicid wasps drag their prey by walking backwards, periodically leaving it unattended to reconnoiter. Many sphecids carry their prey in their mandibles or legs. If they have to dig open their burrow temporary closures, then they may need to leave their prey unattended and exposed to potential enemies. Shifting prey carriage to the middle legs, as is characteristic of the bembicine wasps, frees the front legs to dig without the need to leave the prey unattended. Finally, a few wasps carry their prey on their sting (*Oxybelus*) or in a specialized ant-clamp (*Clypeadon*). Such prey-carriage mechanisms presumably reduce prey loss to foraging ants and other enemies (Evans 1963; Evans and Eberhard 1970), although they note that prey carried on the sting or the ant-clamp are sometimes subject to frequent attacks by Dipteran cleptoparasites.

Males of many solitary wasp species “guard” the nest while the female forages for provisions to stock it with (O’Neill 2001). Although it is thought that the primary benefits for male nest-guarding behavior are associated with paternity assurance (Brockmann and Grafen 1989, 1992), it is likely that an additional offspring benefit from his guarding behavior is to deter parasites and predators, including ants (Brockmann and Grafen 1989; Coville and Griswold 1984; Coville and Coville 1980; Cross et al. 1975; Hook 1984; Iwata 1976; Krombein 1967). Foraging ants and other scavengers and parasites may have been an important factor in the evolution of the subsocial lifestyle of *Xylocopa* and allodapine bees. Although *Xylocopa* is univoltine, even in warmer climates, the mother is generally still alive when her progeny emerge as adults. Some of her adult daughters remain in her nest as guards, at least for a while, until she finishes provisioning. The parent female regurgitates food to the guarding sibling. The multivoltine allodapine bees are similar in that the parent female coexists with her offspring, continuing after they have emerged as adults (Michener 1962). Newly eclosed adults may serve at least two roles, foragers and nest guards while their mother continues oviposit. Although these offspring appear to ultimately go on to become nest foundresses, they may be described as a temporal or phenological caste (Michener 1962, 1974).

Responses to novel Formicidae: The Red Imported Fire Ant

We have reviewed behaviors exhibited by various Hymenoptera that may have evolved in response to ant predation and are, at the very least, currently enlisted as defenses against ants, i.e. the ultimate effects of ant predation on Hymenoptera behavior. Insights into the flexibility of response (i.e. proximate effects of ant predation on

Hymenoptera behavior) may be gained by observing how Hymenoptera respond when exposed to a novel ant species, such as *Solenopsis invicta* Buren, the red imported fire ant (RIFA). Analysis of vertebrate predator/prey relationships has revealed that, although prey that have not been exposed to natural predators for 130 years are much more susceptible to depredation than prey that have been in recent contact with such predators, naïve prey alter their behavior within a generation to become as successful at avoiding predation as their experienced counterparts (Berger et al. 2001). Pimentel (1968) demonstrated that house flies exposed to the parasitic wasp, *Nasonia vitripennis* (Walker), alter behavior and critical life cycle parameters, such as fecundity, within 3 years of exposure, increasing their fitness against *N. vitripennis* compared to the fitness of naïve house flies. This suggests that adaptive behaviors may not be readily apparent in a population but that such behaviors may rapidly appear once a selective force is present. The appearance of the RIFA to the southeast may present a novel threat to many species to which we would expect these species to rapidly develop adaptive behaviors.

However, there is evidence that the RIFA is causing irreparable harm to selected inhabitants of the southeastern U.S. For several years students in the University of Georgia Insect Behavior course observed a ground nesting *Oxybelus* sp. that was abundant on the campus of the University of Georgia. Gradually, the wasp's nests became harder and harder to find, and the local nesting populations appeared to be extinct (R. Matthews pers. comm.). The timing of the disappearance of the wasps coincided roughly with the arrival of the RIFA, in Athens, GA, but there is no direct evidence that the RIFA was responsible for the demise of the wasp. Nevertheless, the RIFA, by virtue

of its aggression and pervasive presence in disturbed habitats, offers an opportunity to assess its potential impact on native fauna.

In its native South America, *S. invicta* is usually restricted to the disturbed habitats along riverbeds. In the southeastern United States *S. invicta* thrives in all types of disturbed habitats, but intact habitats remain relatively fire ant-free. Thus, any impact that the RIFA might have would be greatest on Hymenoptera that nest in disturbed habitats or forage in these disturbed habitats. There is little doubt that ants as voracious as *S. invicta* can have an impact on the potential prey of many solitary wasps (Hu and Frank 1996; Fuller et al. 1997; Hajaj et al. 1997). There is also evidence for various ants that suggest additional importance as competitors for floral resources (Buys 1987; Schaffer et al. 1983; O'Dowd 1979).

Although there are many studies the RIFA and its impact on the fauna of the southeastern United States, most focus on its impact in agroecosystems (Adams et al. 1981; Fuller et al. 1997; Hu and Frank 1996; Russell 1981; Tedders et al. 1990; Yoder et al. 1993), arthropods of medical importance, such as the lone star tick and other ticks (Burns and Melancon 1977; Pavis et al. 1992), or on native ants (Camilo and Phillips 1990; Wojcik 1994). A few studies have investigated effects of the RIFA on vertebrates, such as blue birds, bobwhites, and deer (Allen et al. 1994, 1995, 1997a & b, 1998) but these are not convincing. Studies investigating the impact of RIFA on native Hymenoptera are extremely scarce at the time of this writing. Hymenoptera are an integral part of any ecosystem, filling the niches of predator, pollinator, and parasite. An examination of the possible impacts of RIFA on native Hymenoptera would be important, not only from the perspective of protecting our native fauna, but as a view into the

plasticity of behavior: If Hymenoptera have evolved various behaviors in response to ants, how do these behaviors fluctuate when presented with novel threats, such as RIFA?

Conclusion

It would be naïve to believe that ants have not had an impact on the evolution of Hymenoptera. There is evidence that Formicidae are among the most important mortality factors for many Hymenoptera. There is evidence that Hymenoptera have evolved many traits in response to the predatory pressure of Formicidae, including their behavior, nest architecture, and physiology. Some noteworthy trends include increasing incidence of swarm-founding wasp and bee species in decreasing latitudes (Jeanne 1991; London and Jeanne 2000; Roubik 1989; Wenzel 1991), increasing reliance on glandular repellents in independent-founding wasps (Jeanne 1979; Pardi and Turillazi 1981; Kojima 1993; London and Jeanne 2000), and specialized prey-carriage mechanisms in solitary wasps (Evans 1963; Evans and Eberhard 1970). Some of these trends may simply reflect increased ant pressures in tropical environments (Jeanne 1979; Post and Jeanne 1981; Keeping 1990; Kojima 1992 and 1993; Kudo and Yamane 1996; London and Jeanne 2000). However, little is known about the plasticity of response available to native Hymenoptera when confronted with novel species of Formicidae: What are the repertoires of behaviors that native Hymenoptera may employ when confronted with novel ant species, such as RIFA? There is no work on the proximate effects of novel Formicidae on native Hymenoptera. This information must be estimated from the effects of RIFA on other organisms. Further experimental studies on the potential impact of ants on native wasps and bees are needed. Introduced species such as RIFA offer an

opportunity for such studies, particularly since most previous work has been largely limited to agricultural settings.

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CHAPTER 2

CAVITY-NESTING HYMENOPTERA IN DISTURBED HABITATS OF GEORGIA AND SOUTH CAROLINA: NEST ARCHITECTURE AND SEASONAL OCCURRENCE ¹

Abstract

Trap-nests were used to survey xylophilous (cavity-nesting) wasps and bees in eight early successional clear-cut habitats of northeastern Georgia and northwestern South Carolina during April-September, 2001. Occupants of trap-nests included: three Vespidae (*Euodynerus megaera* (Lepeletier), *Ancistrocerus campestris* (Saussure), and *Monobia quadridens* (L.)); five Sphecidae (*Isodontia mexicana* (Saussure), *Solierella plenoculoides* (Fox), *Trypoxylon collinum* (Smith), *T. clavatum* (Say), and *T. striatum* Provancher); one Anthophoridae (*Xylocopa virginica* (L.)); and two Megachilidae (*Megachile frigida* Smith and *Osmia albiventris* Cresson). Parasites reared from several nests include a *Coelioxys* sp. from nests of *M. frigida*, *Melittobia digitata* Dahms from nests of *T. collinum*, miltogrammine flies from a nest of *I. Mexicana*, and a chrysidid from a nest of *A. campestris*. This study records the first biological data for *S. plenoculoides* and *M. frigida*. Nest architecture (closure plug thickness, presence or absence of vestibules, number and length of cells) is presented with the occurrence and seasonal distribution of these organisms. The bees (*O. albiventris* and *M. frigida*) nested early in the season (April-May), whereas the vespid and sphecid wasps nested predominantly in the summer (May-August). No correlation was found for either the

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number of species nesting per site with either red imported fire ant, *Solenopsis invicta* Buren (RIFA), abundance or plant diversity. However, the four sites in Georgia were more floristically diverse than the four sites in South Carolina and had significantly higher numbers of occupied nests. Only *E. megaera* nested at all sites and it accounted for 35% of all completed nests. Comparisons made with trap-nest data collected 40 years earlier by Krombein (1967) in various southeastern U.S. localities revealed differences that are interpreted in light of nest placement and the arrival of the red imported fire ant, *Solenopsis invicta* Buren. Comparing these data with similar data from trap-nesting studies in Europe suggest that placing more stations with fewer trap-nests per station increases nesting rate (i.e., placing 100 trap-nests at 50 locations will trap more Hymenoptera than placing 100 trap-nests at two locations).

Introduction

Aculeate Hymenoptera are an integral component of most terrestrial ecosystems, including disturbed habitats such as fallow fields, hedgerows and clear-cut forests. Many of them are hunters or parasites of insects and other arthropods, or they fulfill the important function of pollinators. Changes in populations of these Hymenoptera would likely have a cascading effect on other organisms in the community (e.g., prey or even the flora of an area) (Raw 1988; Solbrig 1991; LaSalle and Gauld 1993; Neff and Simpson 1993). Disturbed habitats, such as abandoned fields and early successional stages of clear-cuts, are a prominent habitat type in the southeastern U.S. Both the colonization ability of animals and habitat structure can shape early successional communities. The objective of this study was to survey the xylophilous Hymenoptera

species nesting in disturbed habitats of the Piedmont regions of South Carolina and Georgia. Xylophilous species are excellent subjects for in depth study since they readily accept artificial trap-nests (Krombein 1967). Trap-nesting is a valuable survey tool that yields data on the abundance, phenology, prey, habitat and nest architecture that are not discernible through other methods of surveying hymenopteran populations (Gathmann et al. 1994; Steffan-Dewenter 2002; Miyano and Yamaguchi 2001).

Materials and Methods

Eight sites were selected in Georgia and South Carolina (Table 2.1). All sites consisted of clearings one to four years old on the edge of young pine forests (*Pinus taeda* L.) (Fig. 2.1). To establish the degree of vegetational similarity between the various sites we used Whittaker's Analysis of Diversity (Shmida 1984) (Fig 2.2). All plant species within each of the 1 m² plots were recorded. Plant species located within the 10 m² plot that were not found in the 1 m² plots, were recorded. Plant species located within the 100 m² plot that were not found in any of the plots searched earlier, were recorded. Finally, the entire 1000 m² plot was searched for any plant species not encountered in the earlier searches and these were recorded. The slope of the line of best fit for the cumulative number of species plotted against the area searched on semi-log paper was used as an index of the relative vegetational diversity of each plot.

A line intercept method was used to estimate the percentage of vegetation cover by dominant plants (Bauer 1943). A measuring tape was stretched across a 50 m transect of the plot and the length of tape covering each plant species was recorded and multiplied

by 2 to estimate the percentage cover by that species. All vegetation analysis was conducted in August of 2001.

At each site 20 bamboo stakes, 1.6 meters long, were placed, in pairs approximately 1 m apart, in a transect across the site. Each pair of stakes was approximately 5 m from the next pair. Trap-nests consisted of 6.4 mm, 9.5 mm, and 12.7 mm borings in straight grain pine (2 cm x 2 cm x 10 cm). The borings were made 8 cm deep. Bundles of 3 trap-nests (one of each boring diameter), placed horizontally facing into the clearing, were attached with electrician's tape approximately 1.5 meters above the ground on the bamboo stakes (Fig. 2.3). Nest bundles were placed at each site by the end of February 2001 and the study was concluded at the end of September of the same year.

Every week all nests at each site were examined. Completed nests were removed, labeled with the site, date, treatment and individual nest ID number, and replaced with a nest of the same diameter. Completed nests were X-rayed for 1.5 minutes at 120 v. The nest plug length and number of cells were recorded directly from the radiographs (radiographs were life-sized). The species responsible for making each nest was determined based on nest contents (prey), pupal case morphology, and whenever possible confirmed by rearing nest inhabitants to adulthood. Mold, desiccation, or laboratory infestation by *Melittobia digitata* Dahms resulted in low numbers of emerging adults from many nests. Species were identified by the authors using appropriate taxonomic keys (Coville 1982; Mitchell 1962; Bohart and Menke 1963) and by comparing them with authoritatively identified museum specimens. Voucher specimens are deposited in the Arthropod Collection in the University of Georgia Natural History Museum.

Because the red imported fire ant, *Solenopsis invicta* Buren, (RIFA) is such a prominent predator in disturbed habitats in the southeastern U.S., we measured RIFA abundance four times during the study (once in April, May, June, and August). This was done by placing 10 baited traps on the ground, one between each pair of trap-nest stations at the site (approximately 50 cm from the base of both stations). Baited traps consisted of an open 4 dram vial containing 5 ml of vegetable oil and a piece of dry cat food, Special Kitty® (Fig. 2.4). The vials were placed at 9:00 am and removed and capped at noon of the same day. The number of bait stations at which the RIFA was present was recorded. The mean number of RIFA-infested baits per site was used as a measure of RIFA abundance.

Results

The plant diversity index values of the sites in Georgia (mean = 4.35) were higher than the plant diversity index values for the sites in South Carolina (mean = 1.75) (Table 2.1). The dominant plants at these sites were brambles (*Rubus* spp.), *Lespedeza cuneata*, *Liquidambar styraciflua*, and *Poa* spp. The average abundance of fire ants was variable among sites and sample dates, but was slightly lower overall for sites in South Carolina compared to those in Georgia (Table 2.2). A T-test revealed that, overall, Georgia sites had significantly more trap-nests occupied by Hymenoptera than the South Carolina sites ($P=0.002$) (Table 2.2).

Eleven species of solitary aculeate Hymenoptera completed 255 trap-nests in this study: five sphecid species, three bee species, and three eumenid species (Table 2.3). Of the 735 trap-nests exposed during 2001, 34.7% were occupied. Thirty-five percent of these were used by the eumenid *Euodynerus megaera* (Lepeletier). A sphecid, *Isodontia*

mexicana (Saussure) accounted for 18.8% of all occupied nests, and a bee, *Megachile frigida* (Smith), comprised another 16.4%. Only *E. megaera* nested at all sites and *I. mexicana* nested at all but one site (Table 2.3). Two species, *Xylocopa virginica* (L.) and *Trypoxylon striatum* Provancher, nested at a single site (Table 2.3). X-ray images of some typical nests showing architectural details measured are presented in Fig. 2.5.

The number of completed nests at each site did not correlate to the plant diversity index value ($r^2=0.38$) or to the average abundance of RIFA at that site ($r^2=0.068$). Nor did the number of species nesting at a site have a strong correlation to the site's plant diversity index ($r^2=0.47$) or to the average abundance of RIFA at that site ($r^2=0.13$).

Megachilids (*M. frigida* and *Osmia albiventris* Cresson) occupied nests early in the season (Fig. 2.6). However, megachilids, other than *Osmia* spp., were seen visiting floral resources at the study sites throughout the summer. In contrast, sphecids (*S. plenoculoides*, *I. mexicana*, *T. striatum*, *T. collinum*, and *T. clavatum*) became more prominent later in the season (Figs. 2.7-2.8), as did the eumenids (*E. megaera*, *A. campestris*, and *M. quadridens*) (Fig. 2.9).

Megachilidae: *Megachile frigida* occupied 42 nests at 6 sites (Table 2.3). Nests were mainly constructed in April and May, with a few (probably second generation) being constructed in July. Two *M. frigida* nests had vestibules, both 25 mm in length. Five *M. frigida* nests produced 10 *Coelioxys* (species undetermined) parasites (Megachilidae: Hymenoptera). This species is reported to range from New York to Georgia along the Appalachians (Krombein et al. 1979). For detailed architectural information see Tables 2.4 and 2.10.

Osmia albiventris, a species that ranges from Quebec to Georgia and west to Illinois and Minnesota (Krombein et al. 1979), constructed 8 nests at 3 sites in April and May. These nests were plugged with masticated leaves, with pebbles incorporated. The same material was used to partition off cells, which were provisioned with pollen. For detailed architectural information see Tables 2.4 and 2.11.

Anthophoridae: *Xylocopa virginica* occupied a single nest in June. The nest was in a cavity 12.7 mm in diameter. The plug was relatively thin (1 mm) and the three cells, all containing females, were 19 mm long. This bee ranges throughout the eastern U.S. For detailed architectural information see Table 2.4.

Sphecidae: The most common sphecid nesting in this study was the widely distributed (U.S., east of the Rockies). *I. mexicana* which occupied 48 nests at 7 of the 8 sites (Table 2.3). These nests, easily recognized by the long (3 cm) tufts of grass that protruded from the entrance, began to appear toward the end of May and there appeared to be two generations (Fig. 2.7). No vestibules were found in any of the *I. mexicana* nests we studied. All nests were provisioned with nymphs and adults of *Oecanthus fultoni* Walker. The contents of one nest were consumed by miltogrammine flies (Sarcophagidae: Diptera). For detailed architectural information see Tables 2.4 and 2.7.

The next most common sphecid wasp and the smallest of all species trapped, was *S. plenoculoides*, which constructed 22 nests at 3 sites (Table 2.3). The nests were predominately constructed in 6.4 mm diameter borings (15 nests), with six constructed in 9.5 mm diameter borings and one constructed in a 12.7 mm diameter boring. Nests were lined with small pebbles, twigs, sand, bark and other detritus which served to separate cells. However, the nest architecture of this wasp was too diffuse to measure accurately

so nest dimensions are not reported here. There was an average of 2.67 wasps per nest. Sometimes they were in discrete cells, but just as often they were spread out in a chamber with no discrete cell partitions. Prey were always nymphal acridid grasshoppers approximately 10 mm in length. It is an early season nester, and appeared to have two generations (Fig. 2.7). This species was not reported in Krombein's survey (1967) and is reported to range from New Hampshire, south to Virginia, and west to Colorado, Texas and Arizona (Krombein 1979).

Three species of *Trypoxylon* were trap-nested. All of the nests constructed by *Trypoxylon* species had an interior or preliminary plug, a mud partition against the bottom of the boring placed there prior to provisioning the nest. These spider predators all nested in June and July, with *T. collinum* and *T. clavatum* having a second generation in August (Fig. 2.8). *Trypoxylon collinum* constructed 10 nests at 4 sites (Table 2.3). One *T. collinum* nest had a vestibule 6 mm thick. One *T. collinum* nest was parasitized by *Melittobia digitata* Dahms. This species ranges over the eastern U. S., west to MN and KS (Krombein et al. 1979). For detailed architectural information see Tables 2.4 and 2.8. *Trypoxylon clavatum* occupied 9 nests at 3 sites (Table 2.3). Three *T. clavatum* nests had vestibules, measuring 3, 11, and 5 mm. This species ranges east of the Rockies and has been known to occupy abandoned mud dauber and *Polistes* nests (Krombein et al. 1979). For detailed architectural information see Tables 2.4 and 2.9. *Trypoxylon striatum* occupied 4 nests, all at the same site (Table 2.3). Two nests were in 9.5 mm diameter borings and one nest each in 6.4 and 12.7 mm diameter borings. One *T. striatum* nest had a vestibule whose length was 10 mm.

Eumeninae: All species encountered used mud to partition cells and plug their nests; all preyed on unidentified caterpillars (Lepidoptera). By far, the most common cavity-nester we encountered in this study was *E. megaera*, a species ranging from the eastern U.S. west to Texas and Oklahoma (Krombein et al. 1979). Ninety-one nests were constructed by *E. megaera* starting in late May and lasting through August (Fig. 2.9). Provisioned cells all contained unidentified caterpillars (nest contents were undisturbed so that progeny could develop). Eighty-one of the 91 nests studied had a vestibule. This appeared to be a bivoltine species in our region (Fig. 2.9). For detailed architectural information see Tables 2.4-2.5.

Another eumenid occupying nests in this study was *A. campestris*, which occupied 17 nests at 6 sites (Table 2.3). This wasp ranges from the Rockies to the eastern U.S. and began to construct nests in the middle of June (Fig. 2.9). All provisioned cells contained unidentified caterpillars. Fourteen of the 17 nests constructed by *A. campestris* had a vestibule cell. One of the nests constructed by this species was parasitized by an unidentified chrysidid wasp. This species appeared to be bivoltine in our region (Table 2.9). For detailed architectural information see Tables 2.4 and 2.6.

Only 3 nests were constructed by *M. quadridens* and these were from 3 different sites (Table 2.3). This is the largest eumenine in the eastern United States and it nested only in the largest diameter bores (12.7 mm). Two of the 3 nests had vestibules measuring 45 and 20 mm. Closing plug thickness for these 3 nests averaged 12.67 ± 7.94 mm with a mean of 1.25 ± 0.35 cells per nest (Table 2.4). The mean cell length for the 7 cells measured was 15 mm.

Usurpation could only be determined when a species with noticeably different architectural details (such as mud vs. plant material) usurped a nest under construction or if 2 different species were reared from the same nest. The latter scenario did not occur during our study. A *M. frigida* female usurped an uncompleted eumenid nest (1 eumenid cell). An unidentified *Trypoxylon* species usurped what presumably would have been a nest occupied by an *Osmia* species based on the masticated leaf material and pollen in the unfinished portion of the nest.

In 10 cases nest cavities were sealed with no occupants or provisions. Three were *Isodontia* nests with no occupants or provisions. Another 3 nests, either eumenids or sphecids, were stoppered with mud, but contained no cells or occupants. Finally, 2 nests stoppered with masticated plant material (probably *Osmia* sp.) also contained no cells or occupants. Two nests stoppered with whole leaf discs, indicating a *Megachile* sp., contained no cells or occupants.

Discussion

Eleven species completed trap-nests in our sites. Similar season-long studies in Europe obtained 19 species from 40 old field sites (Gathmann et al. 1994) and 24 species from 15 semi-natural habitats (Steffan-Dewenter 2002). The relative proportion of bees was considerably higher in the European studies (45.8-73.7%) compared to 27.3% in ours. The differences probably reflect relative colonizing ability of species, available cavity sizes and habitat suitability. The European studies lacked the larger cavity size (12.7 mm diameter) available for colonizers whereas our sites lacked the smallest cavity

sizes (2-6 mm diameter). Many of the bees trapped in Europe were small species (e.g., *Heriades* and *Hylaeus*) whereas we trapped more wasps of larger sizes.

Overall, there were significantly more occupied trap-nests at the Georgia sites (70% of all occupied nests) than the South Carolina sites (Table 2.2). This likely reflects that all of the Georgia sites had consistently higher plant diversity indices than the South Carolina sites (Table 2.1), suggesting that local plant community diversity directly influences populations of cavity-nesting Hymenoptera. Although correlations between plant diversity and number of occupied nests or number of species nesting were insignificant, Gathmann et al. (1994) found that plant species richness was the best predictor of the number of species accepting trap-nests in various sites in Germany. Increased plant diversity could increase vegetation structure within a habitat. While vegetation structure was not measured, an increase in 3-dimensional structure would be expected to produce more potential nesting sites for cavity-nesters as well as increasing microhabitats for wasp prey such as spiders, whose web attachments require multiple twigs or leaves.

The overall occupancy rate of nests in this study (34.7%) was surprisingly high. A similar study by Gathmann et al. (1994) had an occupancy rate of less than 1%. Gathmann et al. used reed internode sections for trap-nests and exposed them in only six places at each of their 40 sites, but each placement contained 180 available nests. At each of our eight sites, traps were exposed in 20 different places, but only three traps were available at each placement. The number of completed trap-nests per placement or exposure site over the entire season calculates to 1.22 for Gathmann et al. and 1.59 for this study. The higher number of this study may be explained by the fact that we replaced

nests as they were completed and Gathmann et al. did not. Thus, it appears that the success of the trap-nesting technique for sampling nesting aculeate Hymenoptera is more related to the number of different locations in which traps are placed than to the total number of traps exposed.

In our study 4 species of parasites were reared from the 11 species in the trap-nests (27%): *Melittobia digitata* (Eulophidae) from *Trypoxylon collinum*; unidentified chrysidids from *Ancistrocerus campestris*; unidentified miltogrammine flies (Sarcophagidae) from *Isodontia mexicana*; and *Coelioxys* sp. (Megachilidae) from *Megachile frigida*. Gathmann et al. (1994) reared 4 parasite species from 19 species in their trap-nests in fallow fields (21%), and Steffan-Dewenter (2002) reared 8 parasites from 24 species in trap-nests from semi-natural habitats in Germany (33%). Both European studies obtained proportionately more species of bees than ours.

Because Krombein's detailed trap-nesting study from 1954 to 1962 (1967) was conducted in the same general region as our study, it is worthwhile to compare his results to ours. Krombein obtained 51 *E. megaera* nests at Kill Devil Hills, NC, and Lake Placid, FL, far fewer than the 91 found in our study, considering that he trap-nested over 8 years. In his study these wasps constructed nests in 4.8, 6.4, and 12.7 mm bores, nesting predominantly in 6.4 mm nests. The closure plug thickness for nests in 6.4 mm diameter borings averaged 4 mm, and 8 mm for the 12.7 mm. There were 17 intercalary cells (empty cells between provisioned cells) in the nests in Krombein's study, whereas in our study no nests had intercalary cells. Twenty-one percent of the nests in Krombein's study had vestibular cells, an empty cell immediately after the plug and before the provisioned cells, whereas in our study 88% of the nests had vestibular cells. The mean lengths of the

vestibular cells in Krombein's study for nests 6.4 and 12.7 mm in diameter were 13 and 12 mm, respectively, whereas ours were 10.8 and 25.9 respectively (Table 2.5).

Krombein's traps that contained this species were located on trees in open wooded areas or on the edges of dense woods. Krombein reported that this wasp was bivoltine in the southeastern U.S., which our observations corroborate (Fig. 2.9).

Krombein (1967) obtained 21 nests constructed by *A. campestris*, all at Plummers Island, MD, all in 4.8 mm and 6.4 mm cavities. Again, this wasp was not as common in Krombein's study as it was in ours, considering we trapped 17 nests from this species in a single year. The closure plugs on Krombein's nests averaged 3.4 mm, somewhat less than in our nests (Table 2.4). Eleven of the 13 nests of this species had vestibular cells in Krombein's study.

Krombein obtained 140 nests constructed by *M. quadridens*, all but two in 12.7 mm cavities. This is considerably more than the three nests we obtained in our study. The nests in Krombein's study were constructed at Plummers Island, MD, Kill Devil Hills, NC, and Lake Placid, FL. These wasps also commonly nest in abandoned *Xylocopa virginica* nests (Krombein 1967), sometimes aggressively removing other occupants, such as the giant resin bee, *Megachile sculpturalis* Smith (D. Jenkins unpublished). This wasp was commonly seen visiting flowers at several of our sites. We suspect that this wasp's association with *X. virginica* nests may tend to restrict its nesting habitat to human structures where these nests are now common.

Krombein (1967) obtained only 8 nests constructed by *I. mexicana* during his studies (1967), all in cavities 12.7 mm in diameter, and all from Kill Devil Hills, NC, and Lake Placid, FL. This is considerably fewer than our 48 nests in a single year. It is also

interesting that he trapped more than twice as many *I. auripes* than *I. mexicana*, as we did not obtain a single nest built by *I. auripes*. Nests of *I. mexicana* occasionally made partitions (2 out of 8 nests) in Krombein's study. In our study a slightly higher proportion (22 of 70 nests) had two cells, flimsily separated by grass. The rest of the nests had only one cell, sometimes containing multiple larvae.

Krombein did not report *S. plenoculoides* from his study (1967) and its range is reported to be from New Hampshire, south to Virginia, and west to Colorado, Texas and Arizona (Krombein et al. 1979), so we report a slightly more southern locale for this species. This species reportedly constructs nests in goldenrod galls, among other ready-made cavities (Krombein 1951). Although this wasp was not rare in our study, it was limited to 3 sites and it was abundant at only 2 of these sites. We suspect that *S. plenoculoides* is often unable to aerially transport its prey, which is as large or larger than the wasp, and may crawl with its prey into the trap-nest.

Krombein (1967) obtained 14 nests constructed by *T. collinum*, from Lake Placid, FL, Derby, NY, Plummers Island, MD, and Kill Devil Hills, NC. They nested in 4.8 mm and 6.4 mm cavities, though they preferred the smaller openings, 6 to 1, which may explain why we had relatively few nests constructed by this species since our smallest bore was 6.4 mm. The mean closure plug thickness reported by Krombein for this species was 4 mm, smaller than the mean closure plug thicknesses we report (Table 2.8).

Krombein (1967) collected 139 *T. clavatum* nests from Plummers Island, MD, Derby, NY, and Kill Devil Hills, NC, in cavities 4.8 and 6.4 mm in diameter. In Krombein's study, cells constructed in nests 6.4 mm in diameter averaged 15 mm long. Krombein reported that 48/74 of the nests of this species had vestibules and one nest had

intercalary cells. The mean closure plug thickness reported by Krombein for this species was 4.6 mm, smaller than the mean closure plug thicknesses we report (Table 2.9).

Krombein (1967) obtained 252 nests constructed by *T. striatum*. Nests in his study were constructed at Plummerville Island, MD, Derby, NY, Cropley, MD, and Lost River State Park, WV, and they occupied cavities 6.4, 9.5, and 12.7 mm in diameter

Megachile frigida and *Osmia albiventris* were not reported in Krombein's study (1967). We expected to trap-nest many species of *Megachile* since there are numerous species in our area (Mitchell 1962) and they were common visitors to flowers at all of our sites. We also expected many more species of *Osmia* since these bees were abundant at all of our sites early in the season and were observed visiting flowers of *Rubus* sp. The nesting biology of *Osmia albiventris* was reported by Medler (1967). Three nests obtained in Wisconsin were all in 6.4 mm diameter bores, one of 6 cells, one of 10 cells and one of 4 cells. The cells of the first nest were 4 mm long, except one cell which was 6 mm long, with a 91 mm vestibule and 4 mm plug. The second nest succumbed to mold and its dimensions were not reported. The third nest had cells 9, 8, 11, and 8 mm long, but no plug.

Krombein (1967) obtained 5 nests of *X. virginica*, all in 12.7 mm nests from Plummerville Island, MD, and Lake Placid FL. The closing plugs in Krombein's study ranged from 3-4 mm and cells in the nests he collected ranged from 21-22 mm long. Although this is a common species in the southeastern U.S., it is not surprising that so few nested in our trap-nests. This species prefers to excavate its own cavities or returns to the cavities where it was reared. However, it was often found "resting" in trap-nests. One

to four individuals, both sexes, often were found in the 12.7 mm bores early in the morning.

There are some interesting differences that emerge when our study is compared to the extensive study of Krombein (1967). Three species encountered commonly in our study (*Euodynerus meagera*, *Ancistrocerus campestris* and *Isodontia mexicana*) were less numerous in his study. Furthermore, the Hymenoptera most commonly trapped in Krombein's study (1967) (*Euodynerus foraminatus*, *Ancistrocerus antilope*, *Trypargilum (Trypoxylon) striatum*, *Osmia lignaria*, *Trypargilum (Trypoxylon) clavatum*, *Pachodynerus erynnis*, *Monobia quadridens*, and *Stenodynerus rufulus*) did not appear or were trapped at very low levels in our study. These differences could reflect any number of factors, including habitat selection by the researcher or habitat modification (e.g., an increased area of disturbed habitat), population fluctuations from year to year, or the more widespread prevalence of RIFA in the southeast since Krombein's study.

Krombein's traps were placed in a variety of habitats, including open woods, the edges of woods, and near human habitation and structures, but almost always his traps were placed on buildings or trees. Our traps were placed only in open, disturbed habitats, away from human structures. This could account for a large portion of our differences. For instance, *Osmia lignaria*, which was common in Krombein's study, was never trap-nested in our study, though it is regularly trap-nested on structures in the Athens, GA vicinity (Matthews and Kislow 1972; Mitchell 1962). Krombein's study also revealed a considerable fluctuation in the number of a particular species nesting at a site from year to year. This suggests that, although trap-nesting has been used by many researchers (Fye 1965; Krombein 1967; Danks 1970; Barber and Matthews 1979; Scott 1994, 1997;

Gathmann et al. 1994; Strickler et al. 1996; Tschardt et al. 1998; Frankie et al. 1998; Steffan-Dewenter 2002), there are many aspects to this survey method that require further study. For instance, the matter of trap placement and microhabitat effects are not yet clear and no doubt impact the species nesting at a particular site.

Another important difference between Krombein's studies and ours is the current prevalence of the RIFA in the southeastern U.S. While our data revealed no clear correlation between the numbers or species of cavity-nesting Hymenoptera and RIFA abundance at these sites it seems plausible that the RIFA could have impacted the native insect fauna in these habitats. The RIFA has been present at the Georgia sites since about 1985 (K.G. Ross pers. comm.) and at the South Carolina sites since about 1999 (unpublished observations). To explore the potential impact of the RIFA would require direct comparisons, either between RIFA-infested and non-infested sites or for pre- and post-infestation at the same site.

We found that 88% of our *E. megaera* nests had vestibular cells, whereas only 21% of Krombein's nests had vestibular cells. We also note that the closure plugs in our study tend to be thicker than those reported in Krombein (1967). These differences may reflect pressure exerted by foraging RIFA. Krombein (1967) suggested that the adaptive significance of vestibular cells could be to deter parasites and predators. Nesting females interrupted by foraging RIFA might choose not to provision the last cell and seal off the nest instead. Although there is obviously a high plasticity in nest architecture, such a striking difference may reflect an adaptive behavioral change. There is evidence from other insects that adaptive behavioral modifications can occur relatively rapidly. House flies that were exposed to constant parasitoid pressure from *Nasonia vitripennis*

(Pteromalidae) developed adaptive behavioral traits within three years (Pimentel 1968). Miyano and Yamaguchi (2001) demonstrated that xylophilous wasps preferentially nested in ant-protected nest sites in significantly higher numbers when there was a relatively high density of ant foragers.

It has been shown that behavior modifications induced by the presence of predators can be at least as important as the direct consumption of prey by predators (Beckerman et al. 1997). Thus, additional potential effects of the RIFA on cavity-nesting Hymenoptera in disturbed habitats could be indirect. For example, more mobile prey, such as crickets, grasshoppers, and spiders, are probably able to avoid or escape predation by the RIFA, whereas relatively immobile organisms or life stages (e.g., caterpillars) might be more severely impacted. Although some of the commonest cavity-nesting Hymenoptera in this study were caterpillar predators (e.g., *E. megaera*), it may be that they hunted predominantly in the surrounding forests, thereby avoiding interaction with the RIFA. Ants foraging on nectar-producing flowering plants could conceivably disrupt or stress foraging bees, reducing their pollen and nectar collecting efficiency. While we did not identify pollen and nectar sources for the bees nesting at our site, Gathmann et al. (1994) suggested that bees nesting in habitats with low plant diversity were larger in size and that this enabled them to forage farther from where they nested.

Trap-nesting continues to be an important survey tool in monitoring Hymenoptera diversity, especially as suitable habitat becomes fragmented by human activity and introduced alien species, such as the RIFA, invade habitats. Such studies can also lead to improved conservation of native species, including endangered species. In light of our results we recommend that future trap-nesting surveys include a wide range of boring

diameters (2 mm-9.5 mm) so that a broader and more representative range of taxa will use the nests. We also recommend setting out more trap-nest stations per site, with fewer trap-nests per station, to increase the number of wasps and bees constructing nests.

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Table 2.1. Location and vegetational characteristics for the eight study sites. Sites 1-4 are in northeast GA and sites 5-8 are in western SC.

Site (GPS coordinates)	Plant Diversity Index*	Dominant Plants and % cover**				
		<i>Rubus</i>	<i>Lespedeza</i>	<i>Liquidambar</i>	<i>Poa</i>	Other
Site1 (33.7600°N 83.4364°W)	6.4	15	0	2	0	<i>Helenium</i> (2); <i>Gnaphalium</i> (1)
Site 2 (33.6977°N 83.3750°W)	3.5	16	5	5	0	
Site 3 (33.6863°N 83.3792°W)	5.0	10	0	0	0	<i>Verbascum</i> (2); <i>Cirsium</i> (1)
Site 4 (33.7276°N 83.2595°W)	2.5	0	7	2	4	
Site 5 (34.9162°N 81.9693°W)	2.0	13	8	3	0	
Site 6 (34.9144°N 81.9032°W)	1.0	17	10	2	0	<i>Quercus</i> (1)
Site 7 (34.9768°N 81.8282°W)	2.0	0	0	0	67	
Site 8 (35.0214°N 81.7528°W)	2.0	8	3	3	0	<i>Andropogon</i> (3)

*Whittaker's Analysis of Diversity (Shmida 1984).

**Line transect method (Bauer 1943).

Table 2.2. A site by site comparison of the total numbers of nests completed by all species of cavity-nesting Hymenoptera combined and the mean number of baits (out of a possible ten baits) per site discovered in a 3 hour period by fire ants (*Solenopsis invicta* Buren) at all study sites.

Study site	Total number of completed nests	Number of baits from each sampling date, in chronological order	Mean number of baits discovered by fire ants
1	44	6, 3, 3, 8	5.0
2	47	1, 2, 3, 4	2.5
3	36	3, 2, 7, 0	3.0
4	51	5, 2, 5, 5	4.25
GA Average (per site)	44.5		3.69*
Total	178		
5	13	3, 7, 4, 3	4.25
6	14	0, 3, 1, 2	1.5
7	29	0, 1, 1, 0	0.5
8	21	3, 2, 2, 0	1.75
SC Average (per site)	19.25		2.00
Total	77		

*The mean abundance of the red imported fire ant at GA sites and SC sites was not significantly different in a T-test comparison of means ($P=0.14$).

Table 2.3. The relative abundance of trap-nesting Hymenoptera at each of the study sites.

Species	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Total nests	Number of sites inhabited
<i>Euodynerus megaera</i> (Lepeletier)	24	13	7	26	4	3	8	6	91	8
<i>Ancistrocerus campestris</i> (Saussure)	3	3	1	6	0	2	0	2	17	6
<i>Monobia quadridens</i> (L.)	1	1	0	0	0	0	1	0	3	3
<i>Megachile frigida</i> Smith	10	16	4	5	3	4	0	0	42	6
<i>Osmia albiventris</i> Cresson	0	3	0	0	0	1	4	0	8	3
<i>Xylocopa virginica</i> (L.)	0	1	0	0	0	0	0	0	1	1
<i>Isodontia mexicana</i> (Saussure)	0	6	12	1	6	4	16	3	48	7
<i>Solierella plenoculoides</i> (Fox)	1	0	12	0	0	0	0	9	22	3
<i>Trypoxylon collinum</i> (Smith)	2	3	0	4	0	0	0	1	10	4
<i>Trypoxylon clavatum</i> (Say)	3	1	0	5	0	0	0	0	9	3
<i>Trypoxylon striatum</i> Provancher	0	0	0	4	0	0	0	0	4	1

Table 2.4. The closure plug, vestibule thickness, and cell length (mm) for all species, except *Solierella plenoculoides*. Values are means \pm 95% CI; sample sizes are shown in parentheses.

Species	Plug	Vestibule	Cell	Cell	Cell	Cell	Cell	Cell	Cell
			1	2	3	4	5	6	7
<i>Euodynerus megaera</i>	4.95 \pm 0.33 (91)	13.84 \pm 2.40 (81)	12.09 \pm 1.37 (91)	11.4 \pm 1.42 (90)	11.92 \pm 1.49 (76)	11.08 \pm 1.62 (47)	10.93 \pm 2.18 (27)	11 \pm 2.10 (15)	
<i>Ancistrocerus campestris</i>	4.93 \pm 1.17 (17)	12.57 \pm 4.08 (14)	13.47 \pm 2.67 (17)	12.88 \pm 2.55 (16)	10.83 \pm 3.69 (12)	13.6 \pm 4.15 (10)	6.25 \pm 6.27 (4)	7.75 \pm 5.95 (4)	9 \pm 1.95 (2)
<i>Monobia quadridens</i>	12.67 \pm 7.94 (3)	32.5 \pm 24.49 (2)	22 \pm 9.34 (3)	5 \pm NA (2)	14.5 \pm 14.70 (2)				
<i>Megachile frigida</i>	14.71 \pm 3.04 (42)	25 \pm NA (2)	9.67 \pm 0.32 (42)	10.21 \pm 0.21 (42)	10.43 \pm 0.24 (41)	10.59 \pm 0.25 (38)	10.67 \pm 0.34 (27)	11.09 \pm 0.66 (17)	11 \pm 1.95 (2)
<i>Osmia albiventris</i>	13.88 \pm 5.51 (8)		10.44 \pm 0.62 (8)	10.88 \pm 0.44 (8)	11.44 \pm 0.51 (8)	11.38 \pm 0.64 (8)	11.8 \pm 0.74 (5)	11 (n=1)	12 (n=1)
<i>Xylocopa virginica</i>	1		19	19	19				
<i>Isodontia mexicana</i>	34.29 \pm 2.99 (48)		34.48 \pm 3.26 (48)	23.86 \pm 2.06 (22)					
<i>Trypoxylon collinum</i>	4.91 \pm 0.66 (10)	6 (1)	8.60 \pm 1.06 (10)	12.1 \pm 7.06 (10)	9.80 \pm 2.26 (10)	11.33 \pm 2.75 (9)	7.5 \pm 3.34 (4)	16.5 \pm 6.86 (2)	2 (1)
<i>Trypoxylon clavatum</i>	6.83 \pm 1.34 (9)	6.33 (3)	11.22 \pm 3.85 (9)	12.56 \pm 4.62 (9)	12.88 \pm 3.48 (8)	10.33 \pm 2.27 (6)	5 (1)	6 (1)	
<i>Trypoxylon striatum</i>	5 \pm 0.49 (4)	10 (1)	12 \pm 7.47 (4)	17.25 \pm 5.21 (4)	15.33 \pm 0.66 (3)	15.5 \pm 0.98 (2)			

Table 2.5. The mean closure plug thickness, vestibular cell length, and provisioned cell length for *Euodynerus megaera* nesting in different boring diameters. Ranges are in parentheses.

Bore diameter (mm)	Plug thickness (mm)	Vestibular cell length (mm)	Provisioned cell length (mm)
6.4	4.78 (2-10) n=46	10.76 (2-30) n=37	14.30 (6-29) n=145
9.5	4.68 (3-9) n=37	14.33 (2-48) n=36	10 (5-50) n=167
12.7	5.38 (5-6) n=8	25.88 (7-36) n=8	7.97 (4-28) n=28

Table 2.6. The mean closure plug thickness, vestibular cell length, and provisioned cell length for *Ancistrocerus campestris* nesting in different boring diameters.

Ranges are in parentheses.

Bore diameter (mm)	Plug thickness (mm)	Vestibular cell length (mm)	Provisioned cell length (mm)
6.4	4.11 (2-10) n=9	11.88 (1-20) n=8	16.61 (10-30) n=23
9.5	5.75 (3-10) n=8	13.5 (3-24) n=6	9.36 (5-20) n=42

Table 2.7. The mean closure plug thickness, vestibular cell length, and provisioned cell length for *Isodontia mexicana* nesting in different boring diameters. Ranges are in parentheses.

Bore diameter (mm)	Plug thickness (mm)	Vestibular cell length (mm)	Provisioned cell length (mm)
6.4	29 (25-33) n=2	NA	35.5 (33-38) n=2
9.5	31.53 (10-45) n=34	NA	30.36 (17-56) n=55
12.7	42.33 (10-60) n=12	NA	31.75 (15-50) n=16

Table 2.8. The mean closure plug thickness, vestibular cell length, and provisioned cell length for *Trypoxylon collinum* nesting in different boring diameters. Ranges are in parentheses.

Bore diameter (mm)	Plug thickness (mm)	Vestibular cell length (mm)	Provisioned cell length (mm)
6.4	4.14 (5-10) n=7	NA	11.24 (6-44) n=29
9.5	5.66 (5-6) n=3	6 (6) n=1	8.94 (4-20) n=18

Table 2.9. The mean closure plug thickness, vestibular cell length, and provisioned cell length for *Trypoxylon clavatum* nesting in different boring diameters. Ranges are in parentheses.

Bore diameter (mm)	Plug thickness (mm)	Vestibular cell length (mm)	Provisioned cell length (mm)
6.4	6.38 (3-10) n=8	6.33 (3-11) n=3	12.71 (8-30) n=28
9.5	5 (5) n=1	NA	5.67 (5-7) n=6

Table 2.10. The mean closure plug thickness, vestibular cell length, and provisioned cell length for *Megachile frigida* nesting in different boring diameters. Ranges are in parentheses.

Bore diameter (mm)	Plug thickness (mm)	Vestibular cell length (mm)	Provisioned cell length (mm)
6.4	12.85 (5-24) n=13	25 (25) n=2	10.29 (7-14) n=57
9.5	17.76 (2-43) n=25	NA	10.40 (8-13) n=135
12.7	5.25 (3-8) n=4	NA	10.17 (9-11) n=18

Table 2.11. The mean closure plug thickness, vestibular cell length, and provisioned cell length for *Osmia albiventris* nesting in different boring diameters. Ranges are in parentheses.

Bore diameter (mm)	Plug thickness (mm)	Vestibular cell length (mm)	Provisioned cell length (mm)
6.4	9.13 (6-17) n=6	NA	11.22 (9-12) n=27
9.5	19 (8-30) n=2	NA	11.08 (10-13) n=12



A

B



C

D



E

F



G

H

Figure 2.1. Habitat perspective presented by each study site, showing adjacent forest. Photographs taken in April and May 2001.

A) Site 1, Oconee Co., GA.

B) Site 2, Greene Co., GA.

C) Site 3, Greene Co., GA.

D) Site 4, Greene Co., GA.

E) Site 5, Spartanburg Co., SC.

F) Site 6, Spartanburg Co., SC.

G) Site 7, Spartanburg Co., SC.

H) Site 8, Cherokee Co., SC.

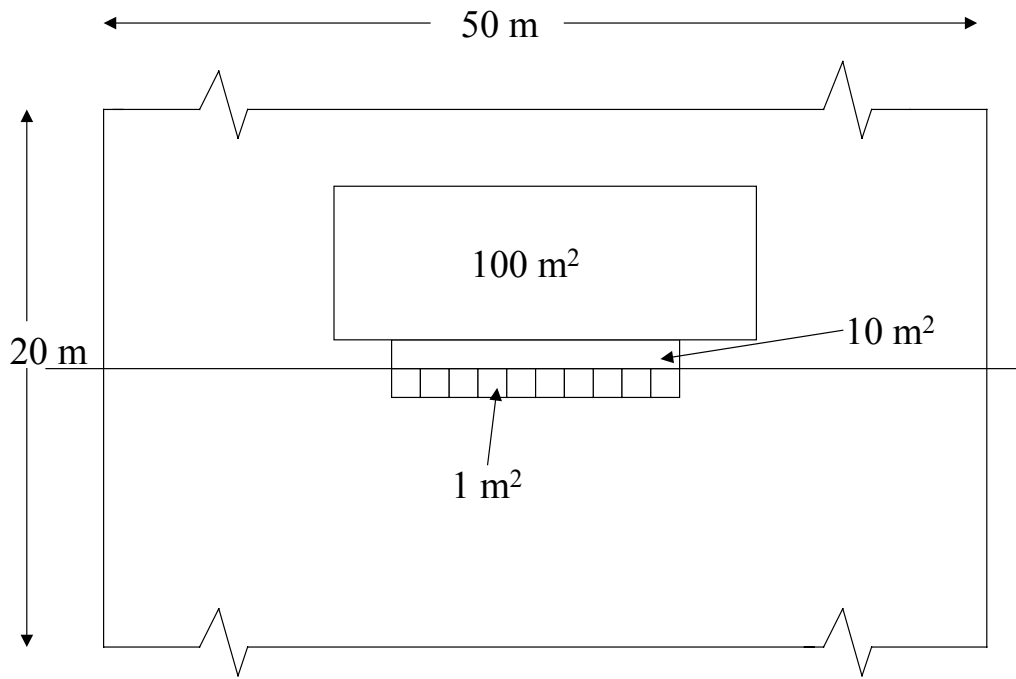


Figure 2.2. Diagram (not to scale) of plant diversity sampling method (Shmida 1984). The cumulative number of plant species in each sample area (1 m², 10 m², 100 m², and 1000 m²) was plotted on a semilog graph. The slope of the line of best fit describes the vegetational diversity of that site.



Figure 2.3. A bundle of trap-nests affixed to a bamboo stake showing the 3 boring diameters.



Figure 2.4. A baited 4 dram vial showing fire ants obtained at the end of a three hour sampling period. Bait consists of vegetable oil and catfood (Special Kitty®) . The mean number of bait stations discovered by RIFA (out of 10) was taken as a measure of RIFA abundance.



Isodontia mexicana



*Solierella
plenoculoides*



*Osmia
albiventris*

Closure
plugs

Cells



*Megachile
frigida*



*Euodynerus
megera*

Vestibular
cell

Preliminary
plug



*Trypoxylon
collinum*

Figure 2.5. Representative X-ray photographs (actual size) of the nests of six of the ten species occupying trap-nests in this study. The architectural features measured are indicated.

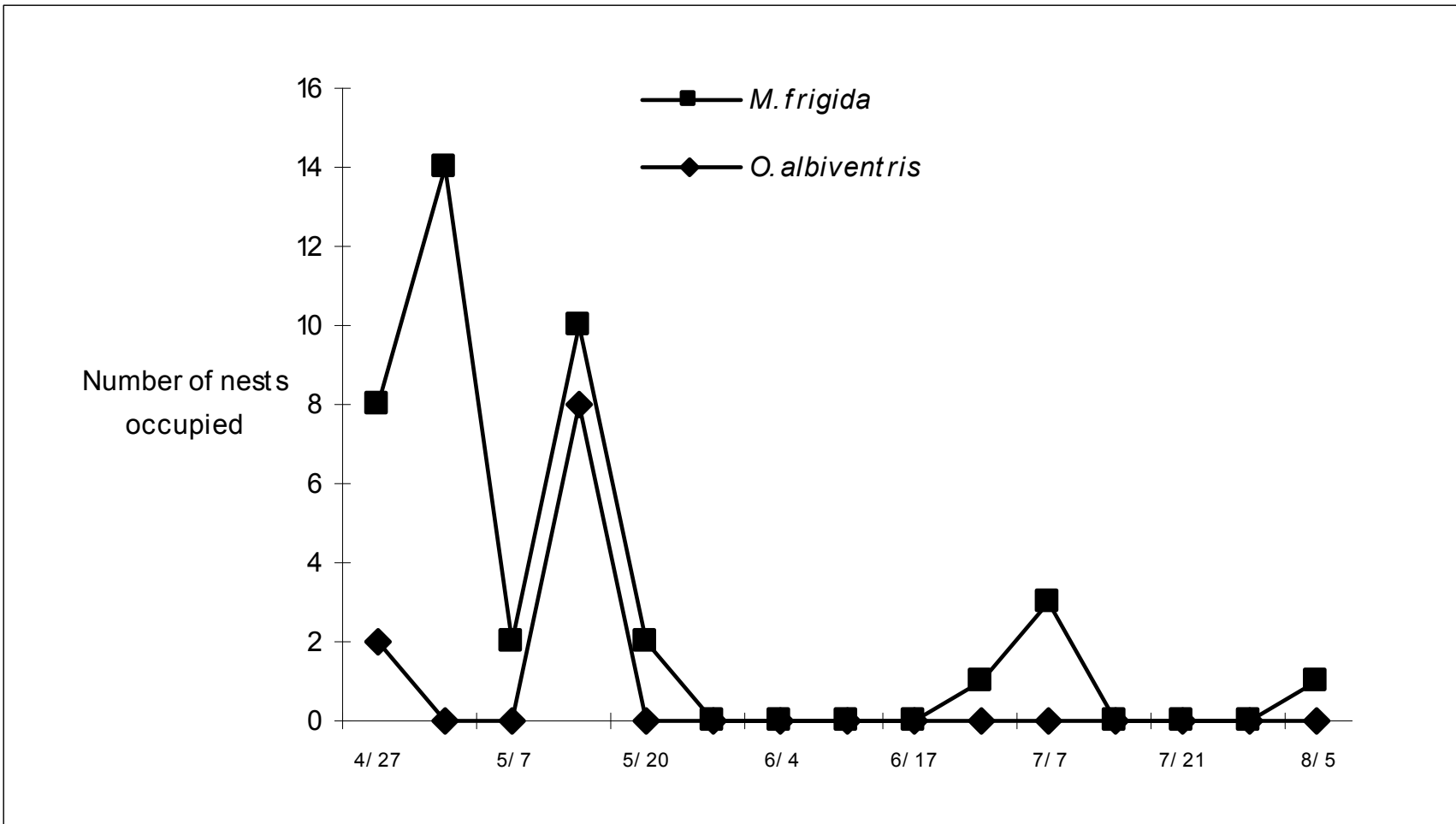


Figure 2.6. Seasonal abundance of *Megachile frigida* and *Osmia albiventris*.

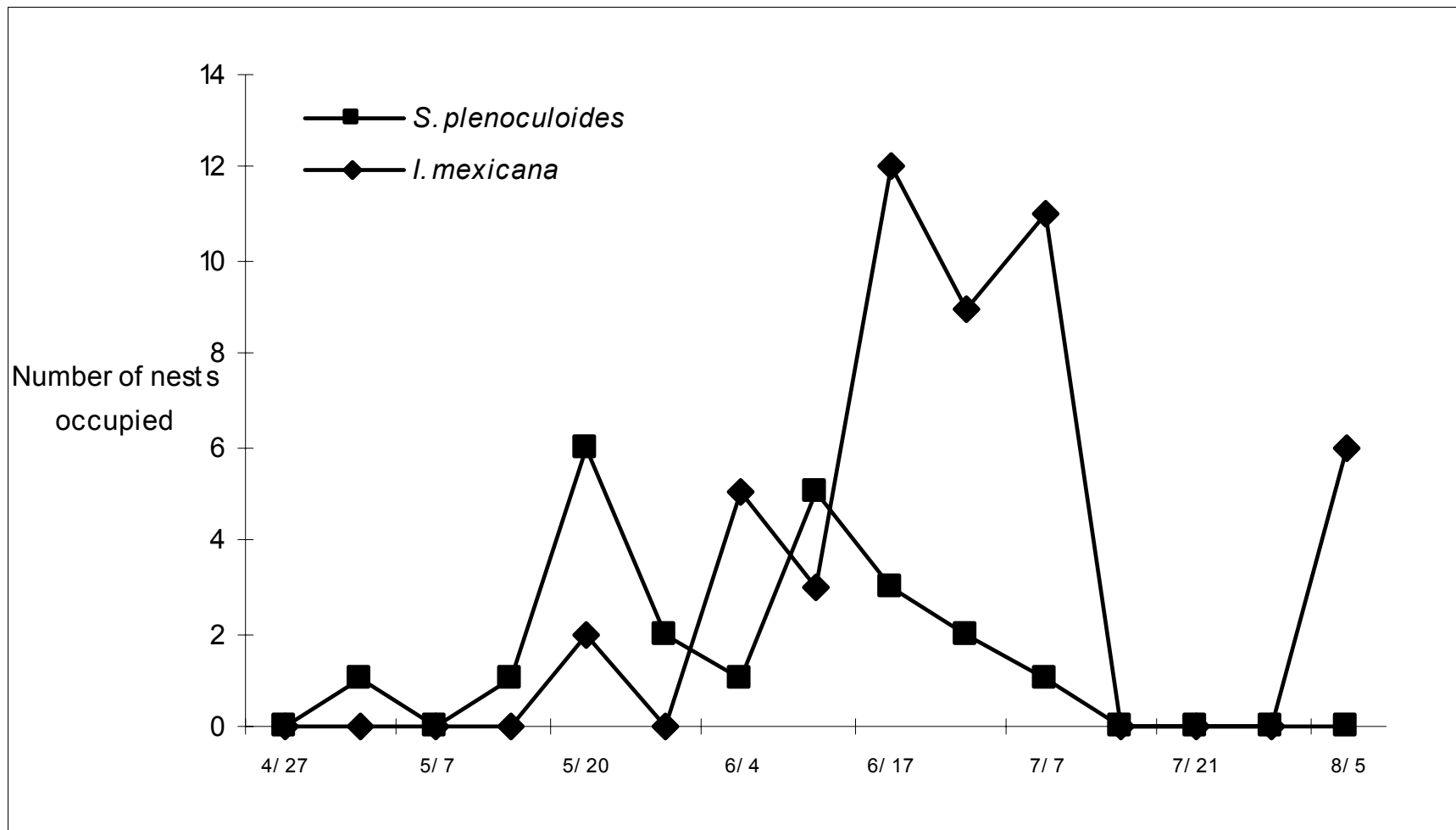


Figure 2.7. Seasonal abundance of *Solierella plenoculoides* and *Isodontia mexicana*.

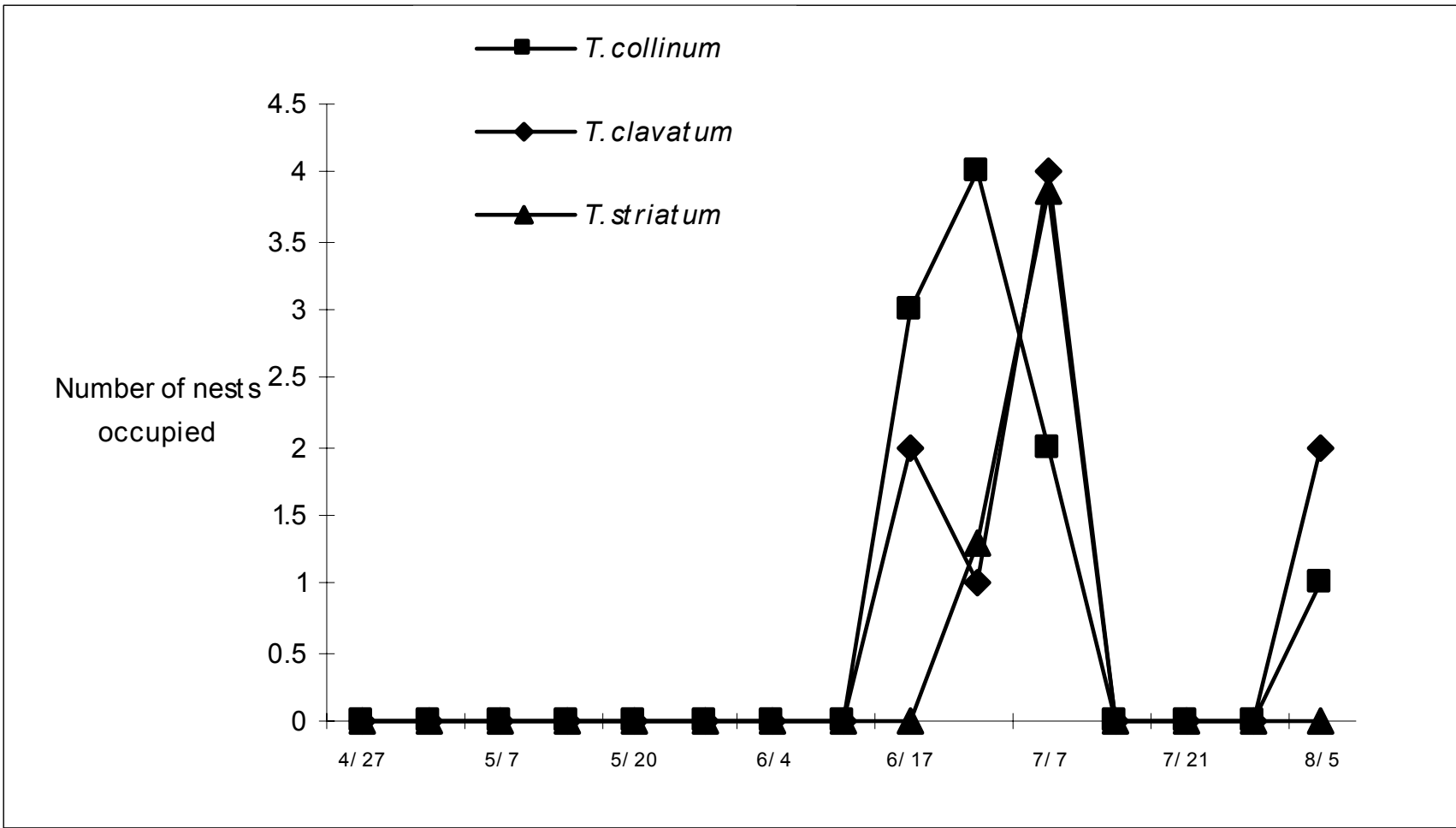


Figure 2.8. Seasonal abundance of *Trypoxylon collinum*, *T. clavatum*, and *T. striatum*.

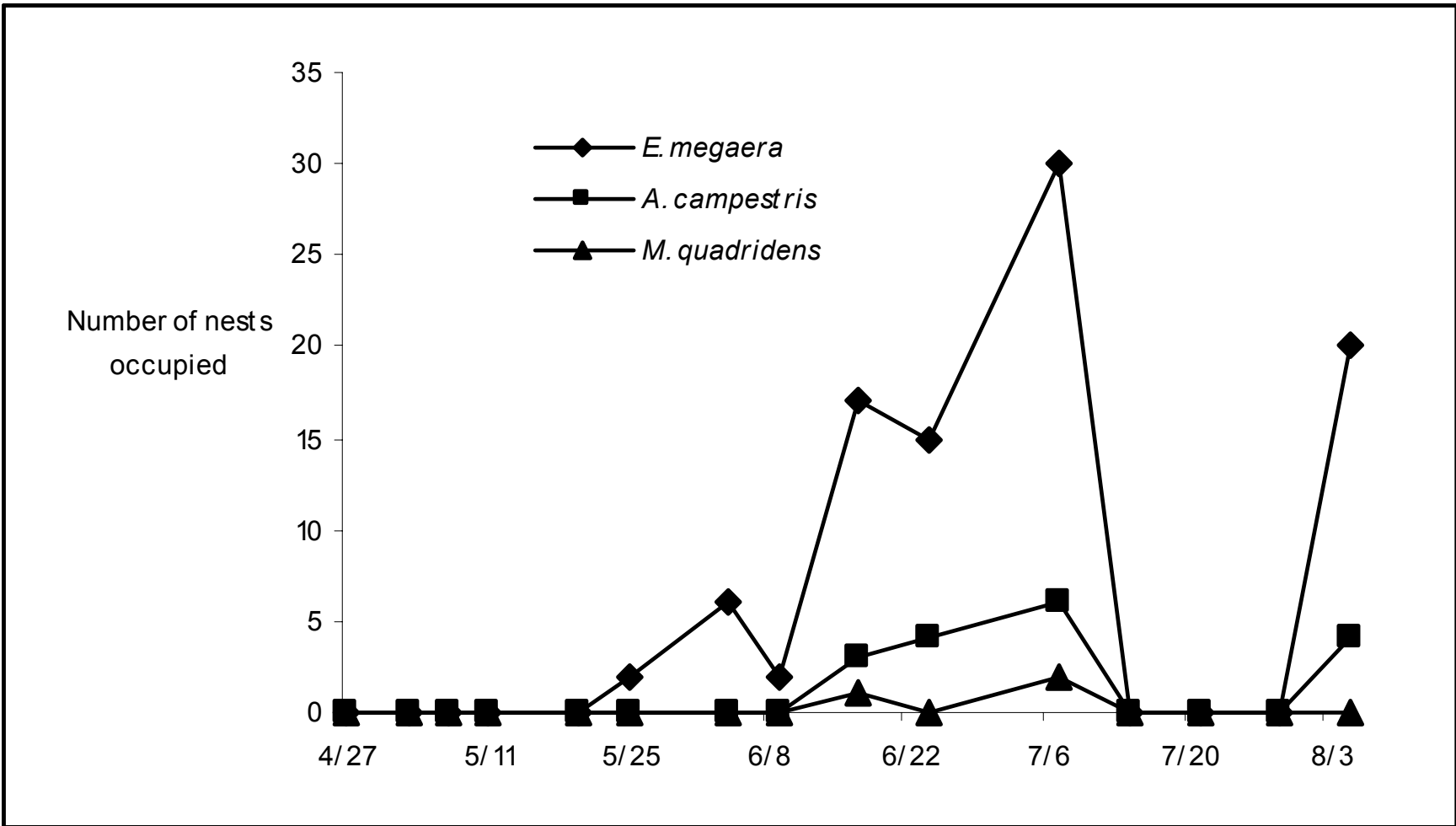


Figure 2.9. Seasonal abundance of *Euodynerus megaera*, *Ancistrocerus campestris*, and *Monobia quadridens*.

CHAPTER 3

NEST CONSTRUCTION IN THE ALFALFA LEAF-CUTTER BEE, *MEGACHILE ROTUNDATA* (HYMENOPTERA: MEGACHILIDAE): EXPERIMENTAL EVIDENCE FOR SHORT TERM BEHAVIORAL ADAPTATION TO FIRE ANTS¹

Abstract

Two groups of alfalfa leaf-cutting bees, *Megachile rotundata* Fabricius, were manipulated to nest in trap-nests at a site in Oconee Co., Georgia which was also monitored for RIFA density. When foraging red imported fire ant (RIFA), *Solenopsis invicta* Buren, densities were lower (spring) there were no significant differences in closure plug thickness and number of cells between nests that were relatively close to the ground (<30cm) and nests 150 cm above the ground. Nor were there any significant differences in closure plug thickness and number of cells between nests in locations protected from ants and nests in locations that were accessible to ants. However, in the summer, when foraging RIFA densities were higher, closure plugs were significantly thicker in nests that were both closer to the ground and accessible to ants than in nests that were further from the ground and protected. There were significantly fewer cells in nests that were closer to the ground than in cells 150 cm above the ground, and significantly fewer cells in unprotected nests than in protected nests. This suggests that these cavity-nesting bees are able to adapt their behavior in response to exposure to a novel Formicidae species.

¹ Jenkins, D.A., and R.W. Matthews. To be submitted to *The Journal of the Kansas Entomological Society*.

Introduction

The red imported fire ant (RIFA), *Solenopsis invicta* Buren, has been spreading throughout the southeastern United States since its introduction at the beginning of the 20th century. RIFA has had a negative impact on native ant species (Wojcik 1994; Camilo and Phillips 1990), arthropods inhabiting dung (Hu and Frank 1996) and a variety of agricultural pests (Russell 1981; Fuller et al. 1997). Ants of several species may exert substantial selective force on ground nesting bees and wasps (Peckham 1977; Cane and Miyamoto 1979; Matthews et al. 1981; Miyano and Yamaguchi 2001).

RIFA are extremely efficient generalist predators that will exploit a wide range of foods. They are ubiquitous in disturbed habitats in the southeastern U.S. However, there are distinct seasonal differences in the density of foraging ants, with typically higher foraging densities as the season progresses (unpublished data).

Potential effects of RIFA on native above-ground nesting bees and wasps have never been investigated. However, the trap-nest technique (Krombein 1967) provides a standard method for systematically sampling xylophilous Hymenoptera (see Chapter 2). Using a commercially available multivoltine species of solitary bee, *Megachile rotundata* (Fabricius), enables experimental manipulation of a population of nesting bees at different seasons at a specific location. Species of insects that nest above ground also present an additional search dimension to foraging ants and other parasitoids and predators. For example, it has been shown that mud dauber wasps (*Sceliphron fistularium* (Dahlbom)) nesting in Jamaica on flat surfaces, such as walls, suffered significantly higher rates of parasitism than wasps nesting on vines (i.e., 2 dimensional surfaces vs. 3

dimensional surfaces). (Freeman 1982). Thus choice of nest location by an above ground nesting bee or wasp could correlate with nesting success.

This study was designed to test the following null hypotheses relating to both seasonal and spatial aspects of the potential interaction between RIFA and the above ground nests of *M. rotundata*:

1) There will be no difference in either number of cells constructed or closure plug thickness in *M. rotundata* nests constructed in ant-accessible vs. ant-excluded sites in either the spring (when foraging RIFA are less abundant) or summer (when foraging RIFA are more abundant).

2) Height of nests above ground will have no effect on the number of cells and nest closure plug constructed in either the spring (when foraging RIFA are less abundant) or summer (when foraging RIFA are more abundant).

3) Nests constructed within treatments (ant-accessible vs. ant-excluded and different heights above the ground) will have no difference in cell number or closure plug thickness between the spring and summer generations.

Materials and Methods

Study Site

Ten nest sites (cinder blocks, 20.32X20.32X50.8 cm) stood on end, each containing 20 horizontally oriented trap nests, 6.4 mm in diameter and 8 cm deep were placed in the cavity of the cinder block and were set up in an open field placed in a row 50 cm apart at the University of Georgia Horticulture Farm in Watkinsville, GA. Five of these nest sites, selected randomly, were moated with a plastic water pan and an application of Tanglefoot® at the base of the cinder block, to prevent access to ants, and

the other 5 were unmoated, allowing access to ants. All trap-nests were within 30 cm of the ground.

A second parallel row of ten more nest sites were set up 5 m from the first. These nest sites consisted of bamboo stakes 1.6 m long each with 20 trap nests of the same dimensions attached to the stake 1.5 m above the ground with the bores facing the east. Five of these nest sites received an application of Tanglefoot® below the trap-nests, to prevent access to ants, and the other 5 nest sites were left untreated so that they were accessible to foraging RIFA (in previous experiments Tanglefoot® did not appear to act as a repellent or an attractant to wide range of xylophilous Hymenoptera).

The Study Species

Diapausing cocoons of the alfalfa leaf-cutter bee, *Megachile rotundata* (Fabricius) (Hymenoptera: Megachilidae), were obtained from a commercial supplier and kept refrigerated. Twenty-eight days prior to the experiment, bees were transferred to a cage at room temperature (24°C) and synchronously reared to produce a cohort of uniformly aged adults in the laboratory. Approximately 200 adults of both sexes (3 days post-emergence) were released in the immediate vicinity of the nest sites before 8:30 am. After 8 days (sufficient time for females to complete a nest) completed nests were removed and split open. The closure plug thickness and the number of cells constructed were recorded. The experiment was run twice, first on April 28th, 2002 (late spring) and again on June 14th, 2002 (early summer).

Measuring the Abundance of Foraging RIFA

To measure the foraging intensity of the RIFA at the study we set out 10 blocks of wood (4 cm by 20 cm) in a line on the ground, 1 m apart. On each block of wood we placed a piece of dry cat food (Special Kitty®) that had been soaked in vegetable oil for 20 minutes. Over the following hour the blocks of wood were continuously monitored for ants. After one hour, the number of blocks that had been discovered by foraging ants was recorded. This protocol was repeated on numerous occasions between April 1st and June 20th, between 8:00 am and 12:00 pm, with the transect of wood block sampling stations in approximately the same locations within the site. For each sampling period the average ambient temperature was also recorded. Data provided a dynamic snapshot of ant foraging intensity and abundance over the time of the experiment. Although Bestelmeyer et al. (2000) review a number of techniques for sampling ants, our method permits a more fine-grained assessment of temporal changes.

Statistical Analysis

A Tukey's Studentized Range Test (SAS 2001) was used to test for differences in mean plug thickness and mean number of cells between treatments and seasons.

Results

RIFA forager numbers were higher in June than in May (Fig. 3.1). However, ant foraging abundance as we measured it did not correlate with temperature ($R^2=0.0089$).

Sixty-three trap-nests were completed by *Megachile rotundata* in the first experiment (early May), 35 in trap-nests that were inaccessible to ants and 28 in trap-nests that were accessible to ants. No significant differences between the mean closure plug thickness of ant-excluded and ant-accessible trap-nests, between the mean number of cells in ant-excluded and ant-accessible nests (Tables 3.1-2) were found. Forty-four bees completed trap-nests in the cinderblocks (<30 cm above the ground) and 19 bees completed trap-nests on the bamboo stakes (150 cm above ground). Again, there was no significant difference between the mean plug thickness of nests constructed 30 cm above the ground and nests constructed 1.5 m above ground, nor was there a significant difference between the mean number of cells in nests constructed 30 cm above the ground and nests constructed 150 cm above the ground (Table 3.3).

Fifty-eight trap-nests were completed by *M. rotundata* females in the second experiment (mid-June). Of these, 39 were in protected locations and 19 were accessible to ants. The mean plug thickness of nests that were ant-excluded from ants was significantly thicker than in nests that were ant-accessible (Tables 3.4-5). The mean number of cells in nests that were ant-excluded was significantly larger than in nests that were ant-accessible (Tables 3.4-5).

Twenty-six bees completed trap-nests that were 150 cm above the ground and 32 bees completed trap-nests that were within 30 cm of the ground. The closure plugs were significantly thicker in nests that were within 30 cm of the ground than in nests 150 cm above the ground (Table 3.6). The mean number of cells in trap-nests within 30 cm of the ground was significantly lower than in nests located 150 cm above ground (Table 3.6). However, these trends were only evident in ant-accessible trap-nest locations (Table 3.6).

Except in one group of nests (ant-accessible/ low nests), plugs were consistently thicker in May than in June. For nests that were ant-accessible and in close proximity to the ground, nests completed in June had significantly thicker plugs in than those completed in May (Table 3.7). Also, except for two groups of nests (ant-accessible/ low nests and ant-excluded/ high nests) there were significantly more cells in nests completed in June compared to those completed in May (Table 3.7). There was no significant difference between the number of cells in nests completed in May and June for ant-excluded/ high nests, but there were significantly fewer cells in nests completed in June compared to those completed in May for ant-accessible/ low nests (Table 3.7).

Discussion

The interactions of ants and aculeate Hymenoptera are complex. There is a strong seasonal effect on RIFA abundance (Fig. 3.1), which, in turn, appears to impact cavity- and, perhaps, ground-nesting Hymenoptera. RIFA is more abundant and poses a greater threat in mid- to late summer than in spring. This is demonstrated by the significant changes in architecture (number of cells and closure plug thickness) that are apparent later in the season. Furthermore, there appears to be a strong 3-dimensional effect on RIFA foraging. Height above the ground appears to play a role in the threat level posed by ant foragers, although we did not sample for foraging ant abundance except on the ground. The significant differences in nest architecture between nests located close to the ground and nests located 150 cm above the ground suggest that RIFA do not forage too far from the ground. However, RIFA can be abundant away from the ground in some cases. We suspect that more natural substrates that rise above the ground, such as trees

and plants, typically have richer sources of food than the bamboo stakes we used. Catalpa trees, for instance, are often covered with foraging RIFA (D. Jenkins unpublished).

Although our data suggests that nests further from the ground were safer from foraging ants it does not appear that the bees preferred to occupy nests in such locations (Table 3.4). The bees did not appear to select where they lived based on perceived benefits. Instead, it is more likely that they constructed nests and, depending on the status of the nest (it's height or whether or not it was protected from ants), were molested by ants and altered their architecture or were left alone and their architecture remained unchanged. The observed changes in nest architecture may have been instigated by contact with a foraging ant. This could be tested in future studies by physically molesting bees constructing nests or exposing them to ants and comparing their nest dimensions to those constructed by bees that were not molested.

It is interesting that, overall, the plug thickness was greater in nests completed in May than in nests completed in June and that the number of cells was higher in nests completed in June than in nests completed in May (Table 3.7). The only treatment that showed the opposite trend was the unprotected/ low nests that presumably were more susceptible to foraging ants. The fact that there are more cells and thicker plugs in the summer if ants are excluded suggests that plug thickness and cell number may be a function of some unidentified parameter besides brood protection. Perhaps gas exchange within the nest is affected by temperature and nest architecture is modified to reflect this. Alternatively, with longer day length, bees could potentially spend more time on nest-construction.

In preliminary tests conducted in August of 2001, 93% of the ant-excluded trap-nests were filled, whereas not a single ant-accessible trap-nest was occupied. Ant-accessible nest were often raided and many nests were never finished due to the persistent foraging of RIFA (D. Jenkins unpublished). Possibly the relatively high density of bee nests in this study increased the likelihood of discovery by RIFA. The well-known recruiting ability of RIFA to food resources (Wilson 1962) may have amplified the impact of foraging ants on our nests. These findings have implications for both gregarious and solitary ground-nesting Hymenoptera, suggesting that they are more at risk from foraging ants than species that nest above the ground. Female *Sphex ichneumoneus* are recorded as nesting in aggregations of up to 50 nests (Bohart and Menke 1963) but such aggregations are difficult to find in the southeastern U.S., even though this species is commonly found at floral resources throughout the summer in the region (D. Jenkins unpublished). It is possible that predatory pressure by RIFA has caused this wasp to nest solitarily.

Finally, it is important to address whether the changes in architecture that we observed were proximate or ultimate evolutionary changes. Although the time period of this study is extremely short (1 season of exposure to fire ants) there is evidence that ultimate evolutionary changes can occur in insects in short periods. Pimentel's work (1968) with *Nasonia vitripennis* and its natural host, the house fly, revealed that house flies exposed to the constant pressure of the parasite reduced their reproductive rate by more than a third compared to naïve house flies and the mean population of the parasite in exposed flies was significantly lower than parasite populations in naïve house fly populations. Even studies on vertebrate predator/prey systems reveal that prey not

exposed to predators for 50-130 years are more vulnerable than “experienced” prey at first, but display altered behavior within a single generation (Berger et al. 2001). Both of these situations may have parallels with the interactions of RIFA and *M. rotundata*. In both cases, there has probably been some exposure to pressure similar to that posed by *N. vitripennis*, vertebrate predators, and the RIFA prior to the experiment. House flies, during their evolutionary history, have been exposed to numerous parasites, including *N. vitripennis*. *Megachile rotundata* has probably been exposed to foraging ants of one species or another during their evolutionary history. Although the RIFA is a novel species to *M. rotundata*, the bee’s evolutionary background had probably equipped it with a repertoire of adaptive behaviors, including plasticity in nest architecture. Selection for these behaviors may be somewhat relaxed when ants do not pose a threat.

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Table 3.1. The effect of accessibility to ants (Tanglefoot®) on *Megachile rotundata* nest architecture (plug thickness and number of cells) for nests constructed in May. Nests within 30 cm off of the ground.

	Mean plug thickness (mm)	Mean number of cells
Ant-excluded (n=28)	9.39 a* ($P=0.61$; $F=0.27$; df=1, 42)	5.04 a ($P=0.91$; $F=0.01$; df=1, 42)
Ant-accessible (n=16)	8.44 a	5.00 a

* Means within a column followed by the same letter are not significantly different (Tukey's Studentized Range Test).

Table 3.2. The effect of accessibility to ants (Tanglefoot®) on *Megachile rotundata* nest architecture (plug thickness and number of cells) for nests constructed in May. Nests 150 cm off of the ground.

	Mean plug thickness (mm)	Mean number of cells
Ant-excluded (n=7)	9.43 a* ($P=0.39$; $F=0.78$; $df=1$, 17)	5.14 a ($P=0.78$; $F=0.08$; $df=1$, 17)
Ant- accessible (n=12)	8.17 a	5.00 a

* Means within a column followed by the same letter are not significantly different (Tukey's Studentized Range Test).

Table 3.3. The effect of height above ground on *Megachile rotundata* nest architecture (plug thickness and number of cells) for ant-excluded and ant-accessible nests constructed in May.

Nest Treatment	Mean plug thickness (mm)		Mean number of cells	
	<u>Low</u> *	<u>High</u>	<u>Low</u>	<u>High</u>
Ant-excluded	9.39 a** ($P=0.99$; F=0.00; df=1, 33)	9.43 a	5.04 a ($P=0.81$; F=0.06; df=1, 33)	5.14 a
Ant-accessible	8.44 a ($P=0.84$; F=0.04; df=1, 26)	8.17 a	5.00 a ($P=1.00$; F=0.00; df=1, 26)	5.00 a

* Low=<30 cm above the ground; high= 150 cm above the ground.

** Means within a row followed by the same letter are not significantly different (Tukey's Studentized Range Test).

Table 3.4. The effect of accessibility to ants (Tanglefoot®) on *Megachile rotundata* nest architecture (plug thickness and number of cells) for nests constructed in June. Nests within 30 cm of the ground.

	Mean plug thickness (mm)	Mean number of cells
Ant-excluded (n=24)	6.42 a* ($P < 0.0001$; $F = 69.81$; df=1, 30)	5.83 a ($P < 0.0001$; $F = 57.66$; df=1, 30)
Ant-accessible (n=8)	16.25 b	3.25 b

* Means within a column followed by the same letter are not significantly different (Tukey's Studentized Range Test).

Table 3.5. The effect of accessibility to ants (Tanglefoot®) on *Megachile rotundata* nest architecture (plug thickness and number of cells) for nests constructed in June. Nests 150 cm off of the ground.

	Mean plug thickness (mm)	Mean number of cells
Ant-excluded (n=15)	6.67 a* ($P<0.62$; $F=0.25$; df=1, 24)	5.33 a ($P<0.02$; $F=6.50$; df=1, 24)
Ant-accessible (n=11)	6.27 a	6.73 b

* Means within a column followed by the same letter are not significantly different (Tukey's Studentized Range Test).

Table 3.6. The effect of height above ground on *Megachile rotundata* nest architecture (plug thickness and number of cells) for ant-excluded and ant-accessible nests constructed in June.

Nest Treatment	Mean plug thickness (mm)		Mean number of cells	
	<u>Low</u> *	<u>High</u>	<u>Low</u>	<u>High</u>
Ant-excluded	6.42 a** ($P=0.68$; F=0.17; df=1,37)	6.67 a	5.83 a ($P=0.08$; F=3.20; df=1,37)	5.33 a
Ant-accessible	16.25 a ($P<0.0001$; F=36.01; df=1,17)	6.27 b	3.25.44 a ($P<0.0001$; F=23.99; df=1,17)	6.73 b

* Low=<30 cm above the ground; high= 150 cm above the ground.

** Means in same row followed by the same letter are not significantly different (Tukey's Studentized Range Test).

Table 3.7. The effect of season, within treatments, on *Megachile rotundata* nest architecture (plug thickness and number of cells).

Treatment	Plug thickness (mm)		Number of cells	
	May	June	May	June
Ant-accessible* / high nests**	8.17 a *** (n=12) ($P=0.05$; $F=4.33$; $df=1,21$)	6.27 b (n=11)	5.00 a (n=12) ($P=0.01$; $F=8.14$; $df=1,21$)	6.72 b (n=11)
Ant-accessible/ low nests	8.44 a (n=16) ($P=0.0005$; $F=16.68$; $df=1,22$)	16.25 b (n=8)	5.00 a (n=16) ($P=0.001$; $F=14.09$; $df=1,22$)	3.25 b (n=8)
Ant-excluded/ high nests	9.43 a (n=7) ($P=0.038$; $F=4.89$; $df=1,20$)	6.67 b (n=15)	5.14 a (n=7) ($P=0.68$; $F=0.17$; $df=1,20$)	5.33 a (n=15)
Ant-excluded/ low nests	9.39 a (n=28) ($P=0.04$; $F=4.44$; $df=1,50$)	6.42 b (n=24)	5.04 a (n=28) ($P=0.003$; $F=9.72$; $df=1,50$)	5.83 b (n=24)

* Ant-accessible = accessible to foraging ants; ant-excluded = not accessible to foraging ants.

** High nests = 150 cm above the ground; low nests = <30 cm above the ground.

*** Means followed by the same letter within a treatment are not significantly different (Tukey's Studentized Range Test).

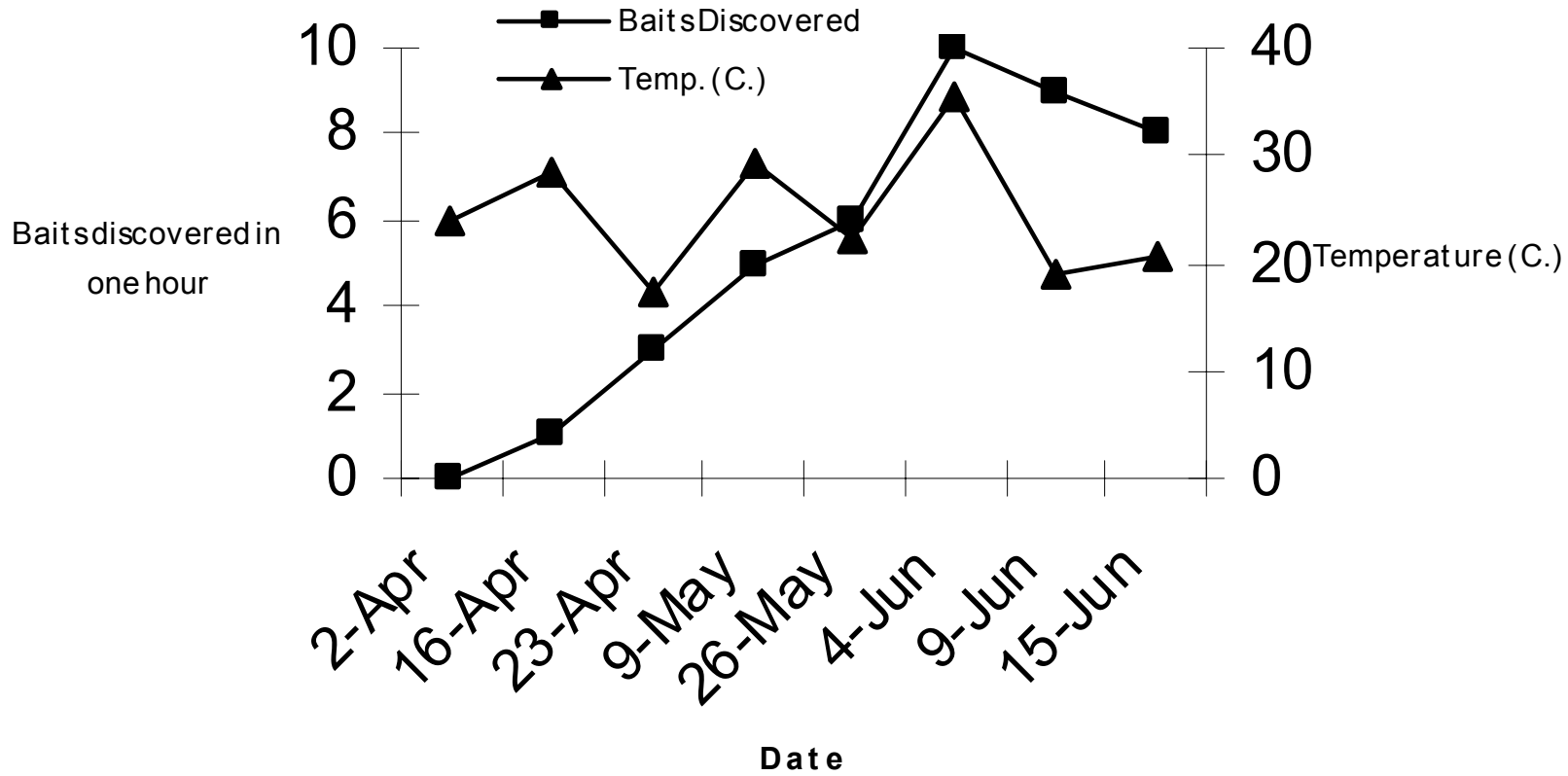


Figure 3.1. The number of baits discovered by *Solenopsis invicta* within an hour (from April to June 2002).

CHAPTER 4

CONCLUSIONS

Ants have been and continue to be an important selective force on many organisms, including social and solitary aculeate Hymenoptera. Nest architecture and glandular physiology of many wasps and bees appear to have been influenced by ant predation (Cane and Michener 1983; Dani et al. 1996; Espelie and Hermann 1990; Turillazzi and Pardi 1981; Hermann and Dirks 1974; Grajales and Wcislo 1998; Jeanne 1970 & 1975; Jeanne et al. 1983; Keeping 1990; Khoo and Yong 1987; Wenzel 1991; Wille and Michener 1973; Williams et al. 1986). Ants are an important source of mortality for many Hymenoptera, particularly ground-nesting species (Peckham 1977; Cane and Miyamoto 1979; Hook and Matthews 1980; Matthews et al. 1981; Kojima 1992; Kojima 1993). Ants also influence diverse aspects of nesting behavior of many social and solitary Hymenoptera (Chadab 1979; Dejean et al. 1998; Dejean et al. 2001; Evans 1963; Herre et al. 1986; Jeanne 1978; Spangler and Taber 1970). A review of the literature on interactions between ants and social and solitary Hymenoptera is presented in Chapter 1 and illustrates a broad range of anti-ant behaviors evolved by these insects.

Our trap-nesting survey of the xylophilous Hymenoptera in early successional stages of old field habitats in Georgia and South Carolina revealed seasonal occurrence and nest architecture for a variety of species, including three Vespidae (*Euodynerus megaera* (Lepeletier), *Ancistrocerus campestris* (Saussure), and *Monobia quadridens* (L.)), four Sphecidae (*Isodontia mexicana* (Saussure), *Solierella plenoculoides* (Fox), *Trypoxylon collinum* (Smith), *T. clavatum* (Say), and *T. striatum* Provancher), two

Megachilidae (*Megachile frigida* Smith and *Osmia albiventris* Cresson) and one Anthophoridae (*Xylocopa virginica*(L.). This study records the first biological data for *S. plenoculoides* and *M. frigida*. The bees (*O. albiventris* and *M. frigida*) nested early in the season (April-May), whereas the vespids and sphecids nested predominantly in the summer (May-August). No correlation was found for either the number of species nesting per site with either red imported fire ant, *Solenopsis invicta* Buren (RIFA), abundance or plant diversity. However, the four sites in Georgia were more floristically diverse than the four sites in South Carolina and had significantly higher numbers of occupied nests. Only *E. megaera* nested at all sites and it accounted for 35% of all completed nests. Comparisons made with trap-nest data collected 40 years earlier by Krombein (1967) in various southeastern U.S. localities revealed nest architecture and species differences that are interpreted in light of nest placement and the arrival of the RIFA. Comparing these data with similar data from trap-nesting studies in Europe (Steffan-Dewenter 2002; Tscharrntke et al. 1998) suggest that placing more stations with fewer trap-nests per station increases nesting rate (i.e., placing 100 trap-nests at 50 locations will trap more Hymenoptera than placing 100 trap-nests at two locations).

The density of foraging RIFA appears to impact the nest architecture of *Megachile rotundata* Fabricius, and their impact appears to lessen the further the bees' and wasps' nests are from the ground (Chapter 3). When RIFA was abundant the bees modified their nest architecture in ways that seem to better protect their progeny (thicker plugs and fewer cells), but only in nests that were close to the ground (within 30 cm). Since RIFA nest in the ground, it is reasonable to assume that foragers would be more abundant on the ground. This suggests that ground-nesting Hymenoptera are potentially

more at risk from ant predation than above ground nesters. Future studies might address the impact that nest aggregation has on susceptibility to RIFA foragers. Also, although methods of baiting for sampling ant species and abundance have been recently reviewed (Bestelmeyer 2000), protocols need to be worked out that more accurately estimate the dynamic threat posed by ants in a particular area. One such method is presented in Chapter 3.

Trap-nesting will clearly continue to be an important survey tool, useful for sampling and monitoring cavity-nesting Hymenoptera in diverse habitats. Base-line studies of native fauna of early successional stages of old field habitats such as were sampled in this study will become increasingly valuable since human activity continues to fragment natural landscapes, and introduced species such as RIFA invade and expand their ranges, impacting native species.

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